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Population Genetic Studies with Sugar Beets (Beta Vulgaris L.) at Different Levels of Soil Fertility[1]

LeRoy Powers, D. W. Robertson, Robert S. Whitney, and Willard R. Schmehl[2]

Introduction

The increased use of nitrogen fertilizers by farmers has emphasized the need for information concerning the effect of different levels of soil fertility on the efficiency of breeding programs. Also, the increased use of nitrogen fertilizer in many growing seasons and certain areas in most growing seasons has resulted in decreased percentage sucrose in sugar beets. Hence, information is needed as to the part that plant breeding may have in helping to overcome this problem of decrease in percentage sucrose. This raises the problem as to what level of soil fertility the breeding programs should be conducted. It was decided to conduct population genetic studies with sugar beets (*Beta vulgaris* L.) at two different levels of soil fertility for the purpose of obtaining information leading to the solution of these problems and others set forth in the next paragraph.

Selection experiments were included with the population genetic studies at different levels of soil fertility to determine the following: The effectiveness of methods for identifying genetically-superior individuals (Powers, 9, and Powers, et al, 12)[3], the the feasibility of increasing both percentage sucrose and weight per root simultaneously, and the efficiency of the polycross method (Tysdal, et al, 15) in testing the merits of those mother beets selected from small unit areas as genetically-superior (see Powers, 9, page 429).

The studies were conducted during 1956 and 1957.

Materials, Experimental Design, Methods, and Analyses

Materials

The materials used in the study are populations and fertilizer treatments. The populations are A54-1, A54-1BB, 50-406BB, 50-406, F_1 hybrid, and 52-307. A54-1 is a commercial variety and A54-1BB resulted from seed harvested from 25 mother beets of A54-1. The 25 mother beets giving rise to population A54-1BB

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[2] Geneticist, Crops Research Division, Agricultural Research Service, U. S. Department of Agriculture, Professor and Head, and Professors, Agronomy Department, Colorado State University, respectively.

[3] Numbers in parentheses refer to literature cited.

were grown in an isolated seed plot along with 25 mother beets from each of 22 other populations. This isolation plot was composed of 25 rows in each of which one mother beet from each population occurred at random, making a total of 23 mother beets per row. Seed was harvested from all mother beets on an individual plant basis and seed was bulked to provide population A54-1BB. Seed from each mother beet of A54-1 was bulked and thoroughly mixed to produce the seed lot from which A54-1BB was grown. Seed saved from mother beets of 50-406 and handled in a similar manner produced the population designated as 50-406BB. It was hoped that seed of A54-1BB produced in such a manner would have a broader genetic base than the corresponding commercial variety. Populations 50-406 and 52-307 are inbreds and the F_1 hybrid population resulted from crossing them. The inbred 50-406 has green hypocotyls and 52-307 has red hypocotyls. The seed used to produce the F_1 hybrid plants was harvested from mother beets of 50-406 and the plots of the F_1 hybrid population were thinned to red hypocotyl plants.

There were two treatments, fertilized and non-fertilized. The fertilized plots received a surface application of 100 pounds of N and 250 pounds of P_2O_5 per acre on April 4, 1956. The fertilizer was cultivated under with a rototiller. The experiment was planted on April 10 and 11. On June 26, another 100 pounds of N per acre was drilled in the center of each space between rows of the fertilized plots.

Experimental Design

The experimental design is a "split-split plot" (see Federer, 2). The design of the experiment can be explained more readily by listing the sources of variation designated as main effects (see Table 1).

As shown in Table 1 there are 40 replications. Treatments are a split plot of replications, the two treatments having been randomized within each replication. The six populations are randomized within each treatment and the eight locations are within each plot of each population. Each location is composed of a single plant. The plant genotypes in this experiment could not be identified. In other experiments where marker genes are employed they can be identified and were found to occur at random within the plot (see Powers, 6). The plots were single rows running north to south. Hence, any differences due to locations represent a gradient running from north to south. Hence, locations are a split plot of populations and the design is a split-split plot.

Table 1.—Sources of Variation Designated as Main Effects, and Number of Each.

Main Effects	Number
Replications	40
Populations	6
Treatments	2
Locations	8

Every plot was bordered by a row of A54-1. After thinning, each plot had 12 plants and the stand remained excellent during the growing season. Data were taken on only eight plants, the extra plants at each end of the plot being discarded at time of harvest. The rows were spaced 22 inches apart and the plants were thinned to a spacing of 20 inches within the row. Selection was avoided during thinning by saving the plant farthest south in a "blocked group."

The design of the experiment for the polycross test of the progenies from 32 selected mother beets is very similar to that employed by Powers, Finkner, Doxtator, and Swink (10). The 32 selections are divided into three groups of 10, 10, and 12. Then to each group were added two entries of A54-1. These three groups are designated as blocks 1, 2, and 3. Hence blocks 1 and 2 are composed of a total of 12 entries and block 3 had 14 entries. The design differs from that previously given by Powers et al (10) in that the same entries occur together in the same block in all replications. Entries are randomized within blocks, and blocks are randomized within replications. There is a total of five replications.

Methods

The characters reported in this study are percentage sucrose, weight per root, and parts per million of NO_3-N in the petioles. Percentage sucrose was determined from the leaded filtrate by methods standard with sugar companies. The individual root formed the basis of the analyses. The root was obtained by the standard topping process which removes all leaves and the crown of the beet. The weight per root is that of the topped beet and is measured in pounds. The roots were weighed just before rasping to obtain the pulp for sucrose analyses.

The petiole samples used to determine parts per million of NO_3-N were taken on October 1. Harvest of the experiment started on October 8 and was completed on October 9. The petioles were not taken on the basis of individual plants but on the basis of 32 plants from four contiguous replications. The samples were taken from within replications, populations, and

treatments. The method of taking samples for NO_3-N analyses of the petioles can be grasped more readily by considering Diagram 1.

Diagram 1 depicts the actual field planting arrangement of the replications and fertilizer treatments. Four replications entered into each sample taken from each population and treatment for NO_3-N analyses of the petioles. For example, considering the population A54-1 fertilized sample, there are four F plots each having eight plants. This makes a total of 32 plants per sample. Hence, since there are two treatments and six populations there is a total of 12 samples per group. Since there are 40 replications there are 10 such groups, each composed of 12

Diagram 1.—Diagram of field plan.

Series Number	Replication and Treatment			
1	1 F	NF	2 F	NF
2	NF	4 F	F	3 NF
.	. .	. .	. .	. .
.	. .	. .	. .	. .
.	. .	. .	. .	. .
19	37 F	NF	38 NF	F
20	F	40 NF	F	39 NF

samples. Only one petiole was taken from each of the 32 plants making up any given sample. Replications 1 to 4, inclusive, composed the first group and so on up to replications 37 to 40 which composed the tenth and last group.

Analyses

In this study it is of biological interest to know if differences between mean values of main effects exist, if there are interactions between main effects, if there are differences between mean variances, if the residual variances are significantly different from zero, and, if so, which are the greater. If the residual variances of the segregating populations are found to be significantly different from zero, then the frequency distributions become of interest and will be studied.

The analysis of variance is employed to test significance of differences between means and variances. Chi square is used to determine whether differences noted in frequency distributions are statistically significant. The standard error of the binomial distribution is used to test the significance of differences between numbers (see Snedecor, 14). Regression of the variance on the mean is used to estimate the environmental variances for weight per root, using the data for the two inbreds and their F_1 hybrid. For details of the methods used in this article see Powers (7, 9), Powers, et al (11), Powers, Robertson, and Remmenga (13), and Powers, Robertson, and Clark (12).

Results

The results will be discussed under the general headings, means, variances, frequency distributions, and progeny tests. The means and variances will be further divided into main effects and interactions.

Means

Analyses of variance

The analyses of variance for percentage sucrose and weight per root are given in Table 2. The smaller mean squares used to calculate the F values are designated by the letters in column 2 and the letters following the F values in columns 6 and 7. Whether there are significant differences of main effects and of interactions can be determined by comparing the F values in columns 6 and 7 with those in columns 8 and 9.

Considering percentage sucrose there are significant differences for replications, populations, and treatments. There are significant differences in respect to the first order interactions R X T, R X L, and P X T. This means that within their corresponding interactions there are significant differences between replications, populations, treatments, and locations. Likewise

Table 2.—Analyses of Variance for Percentage Sucrose and Weight Per Root.

Source of Variation	Smaller M. S.[1]	Mean Square		F Value[2]			F Value at Level of	
		Sucrose	Weight	D. F.[1]	Sucrose	Weight	1%	5%
Replications		82.0306	1.8020	39	4.67b	1.05b	2.11	1.69
Populations		105.4703	243.1541	5	24.24a	429.98a	3.11	2.26
Treatments		378.8222	379.5072	1	21.55b	220.22b	7.31	4.08
Locations		4.2240	0.7077	7	2.03c	2.01c	2.73	2.05
R X P	a	4.3514	0.5655	195	1.15d	d	1.39	1.26
R X T	b	17.5806	1.7233	39	4.63d	2.82d	1.69	1.45
R X L	c	2.0771	0.3520	273	1.31e	1.02e	1.28	1.19
P X T		61.6381	7.1904	5	16.24d	11.78d	3.11	2.26
P X L		1.2884	0.4390	35	f	1.30f	1.69	1.45
T X L		0.9306	0.2561	7	f	f		
R X P X T	d	3.7954	0.6106	195	2.86g	1.76g	1.28	1.19
R X P X L	e	1.5799	0.3458	1365	1.19g	g	1.11	1.08
R X T X L	f	4.1607	0.3386	273	3.14g	g	1.28	1.19
P X T X L		1.6628	0.4513	35	1.25g	1.30g	1.71	1.47
R X P X T X L	g	1.3255	0.3460	1365				

[1] M. S. designates mean square and D. F. degrees of freedom.
[2] The letter after the F value indicates the smaller mean square used in calculating F.

there are significant differences for the second order interactions R X P X T, R X P X L, and R X T X L. Again all of the main effects show significant differences within the second order interactions in which they occur. Those interactions expected to provide information of greatest biological importance involve replications, populations, and treatments either as first or second order. The interaction of replications × populations × treatments might be expected to furnish more valuable information than any of the first order interactions.

For weight per root there are significant differences for populations and treatments. The F values for the first order interactions R × T and P × T show that all replications are not behaving the same in respect to all treatments. The F value for the second order interaction of replications × populations × treatments confirms that there are significant differences between the behavior of the main effects involved. None of the F values for weight per root indicate significant differences between locations.

The analysis of variance for parts per million of NO_3-N in the petioles is given in Table 3. A comparison of F values for main effects shows that there are significant differences for replications and populations. The F value for replications × treatments shows that treatments are not behaving the same in all

Table 3.—Analysis of Variance for Parts Per Million of NO_3-N in the Petioles.

Source of Variation	Smaller M. S.[1]	Mean Square	D. F.[1]	F Value[2]	Level of F Value at 1%	Level of F Value at 5%
Replications		183,571,989.9	9	5.52b	5.35	3.18
Populations		7,083,179.6	5	4.95a	3.46	2.43
Treatments		164,898,063.0	1	4.96b	10.56	5.12
R X P	a	1,431,316.6	45	1.72d	2.06	1.66
R X T	b	33,272,576.7	9	39.88d	2.84	2.10
P X T		2,453,922.4	5	2.94d	3.46	2.43
R X P X T	d	834,300.8	45			

[1] M. S. designates mean square and D. F. degrees of freedom.
[2] The letter after the F value indicates the smaller mean square used in calculating F.

replications. The F values for replications × populations and populations × treatments are significant at the five percent level.

The above analyses of variance have their greatest importance in showing that a study of both main effects and interactions probably will provide biological information of importance. The mean squares of these analyses can be used in tests to determine which means are significantly different.

Main effects

The means of the main effects are listed in Table 4. The characters are percentage sucrose, parts per million of NO_3-N in the petioles, and weight per root. The replications have been collected into five groups, each composed of eight replications. The purpose of this grouping was to more clearly portray differences between replications as regards parts per million of NO_3-N in the petioles and to show the relation between this character and percentage sucrose, and this character and weight per root.

A study of the means of Table 4 reveals the following. For percentage sucrose, replication groups 25 to 32 and 33 to 40 are lowest, whereas replication groups 9 to 16 and 17 to 24 are highest. For parts per million of NO_3-N in the petioles the first three replication groups are lowest and the last two are highest, the 33 to 40 or last group being extremely high. For weight per root the first and last replication groups are highest. Considering populations the inbreds 50-406 and 52-307 are lowest in percentage sucrose, 50-406 is lowest in parts per million of nitrate nitrogen, and A54-1 and A54-1BB are highest in weight per root. The non-fertilized plots are highest in percentage sucrose and lowest in parts per million of NO_3-N and weight per root. These findings of significant differences between main effects justify

Table 4.—Means of Percentage Sucrose, Parts Per Million of NO_3-N in the Petioles, and Weight Per Root for Replication Groups, Populations, and Treatments.

Main Effects	Sucrose	NO_3-N	Weight
	%	p.p.m.	Lbs.
Replication groups			
1-8	17.3	818	1.72
9-16	17.9	653	1.60
17-24	17.7	729	1.49
25-32	17.1	1685	1.59
33-40	15.8	8909	1.77
Populations			
A54-1	17.3	2985	2.26
A54-1BB	17.3	3238	2.18
50-406BB	17.4	2879	1.72
50-406	16.8	1630	0.89
F_1 hybrid	17.6	2172	1.88
52-307	16.6	2448	0.87
Treatments			
Fertilized	16.8	3731	1.95
Non-fertilized	17.5	1386	1.32
Mean	17.2	2559	1.63

a further study of Table 4 to ascertain the interrelations between the three characters. In fact the main interest is in the interrelations.

Without exception a decrease in the parts per million of NO_3-N in replication group means is accompanied by an increase in percentage sucrose of replication group means. The same tendency is noted between weight per root and percentage sucrose. As might be expected there is a tendency for weight per root and parts per million of NO_3-N in the petioles to be positively associated. The same relations hold for the comparison listed under treatments.

The relation noted between percentage sucrose and parts per million of NO_3-N in the petioles for replication and treatment means does not seem to hold so well for population means. However as regards these population means a tendency for a positive relation between weight per root and parts per million of NO_3-N in the petioles does exist. Another point of interest and probably of considerable economic importance is a comparison between the means involving the F_1 hybrid and the two inbred parents 50-406 and 52-307. The F_1 hybrid exceeds either parent in percentage sucrose.

Hence heterosis for percentage sucrose is definitely expressed in the F_1 hybrid involving the inbred lines 50-406 and 52-307.

These data are for 1956. In a 12 by 12 latin square test conducted in 1957 the percentage sucrose for the F_1 hybrid involving these same two inbred lines was higher than that of either parent. Hence, that heterosis for percentage sucrose does occur in certain hybrids under the conditions of the growing seasons of 1956 and 1957 on the Agronomy Farm at Fort Collins, Colorado, is definitely established. Other hybrids in tests at Fort Collins conducted by the senior author support this finding. Similar results (unpublished data) have been obtained by Rush and Oldemeyer of the Amalgamated Sugar Company in Idaho and Peterson of the Holly Sugar Company in Wyoming. It seems that heterosis for percentage sucrose in F_1 hybrids involving inbred lines of sugar beets may not be uncommon. This fact may prove to be of considerable economic importance in the production of beet sugar.

A comparison between the F_1 hybrid and the two inbred parents as to parts per million of NO_3-N in the petioles furnishes some evidence as to phenotypic dominance relations. The mean of the two inbreds (see Table 4) is 2039. The mean of the F_1 hybrid, 2172, is not significantly different from 2039. Dominance is not complete and there is no heterosis, and the true situation may be either partial dominance of greater parts per million of NO_3-N in the petioles or intermediate dominance. The weight per root for the F_1 hybrid is approximately twice as great as that of either inbred parent. Heterosis of weight per root was to be expected.

First order interactions

The means for percentage sucrose, parts per million of NO_3-N in the petioles, and weight per root for the interaction of replications $\times$ populations are listed in Table 5.

It can be seen from Table 2 that the interaction of replications $\times$ populations was not statistically significant at the five percent level for either percentage sucrose or weight per root.

This does not hold for NO_3-N, as this interaction for parts per million of NO_3-N in the petioles was significant at the five percent level (see Table 3). In other words all varieties were not behaving the same for all replications in respect to the amount of NO_3-N in the petioles. The inbred 50-406 seems to be responding differently than the other populations to replication groups 25 to 32 and 33 to 40. This is most clearly evidenced in comparing populations 50-406, F_1 hybrid and 52-307. Inbred 50-406 does not differ materially from the F_1 hybrid and 52-307 in groups 1 to 8, 9 to 16, and 17 to 24, but is lower in parts per million of NO_3-N in the petioles for groups 25 to 32 and 33 to 40.

Table 5.—Means of Percentage Sucrose, Parts Per Million NO_3-N in the Petioles, and Weight Per Root for the Interaction of Replications X Populations.

Population and Character	Replication Groups				
	1-8	9-16	17-24	25-32	33-40
A54-1					
Sucrose, %	17.6	18.0	18.0	17.5	15.6
NO_3-N, p.p.m.	1198	901	734	2174	9916
Weight, lbs.	2.42	2.10	2.01	2.23	2.56
A54-1BB					
Sucrose, %	17.4	18.4	18.1	16.8	15.8
NO_3-N, p.p.m.	1002	928	983	3097	10182
Weight, lbs.	2.34	2.04	1.99	2.14	2.37
50-406BB					
Sucrose, %	17.5	18.0	18.0	17.4	16.2
NO_3-N, p.p.m.	991	728	956	1612	10108
Weight, lbs.	1.76	1.84	1.64	1.58	1.77
50-406					
Sucrose, %	17.4	17.3	17.2	16.4	15.6
NO_3-N, p.p.m.	616	494	496	663	5880
Weight, lbs.	0.95	0.85	0.83	0.88	0.92
F_1 hybrid					
Sucrose, %	17.9	18.4	18.0	17.3	16.4
NO_3-N, p.p.m.	543	382	586	1240	8109
Weight, lbs.	1.94	1.94	1.70	1.85	1.99
52-307					
Sucrose, %	16.2	17.4	17.1	16.9	15.2
NO_3-N, p.p.m.	558	484	620	1322	9259
Weight, lbs.	0.90	0.82	0.76	0.88	1.00

If further research confirms this differential behavior between populations it may have considerable importance in breeding varieties adapted to production at different levels of nitrogen fertility.

The means for percentage sucrose, parts per million of NO_3-N in the petioles, and weight per root for the interaction of replications $\times$ treatments are listed in Table 6. This interaction is highly significant for all three characters. For the first three replication groups the two fertilizer treatments do not differ greatly in percentage sucrose but they do differ materially in the last two replication groups. For NO_3-N there is a decided increase in replication group 25 to 32 on the fertilized plots, whereas such is not the case for the non-fertilized plots. For weight per root on the non-fertilized plots there is a decided increase in replication group 33 to 40 over all other groups but on the fertilized plots the 33 to 40 group does not differ appreciably from the others in weight per root.

Table 6.—Means of Percentage Sucrose, Parts Per Million NO_3-N in the Peticles, and Weight Per Root for the Interaction of Replication X Treatments.

Treatment and Character	Replication Groups				
	1-8	9-16	17-24	25-32	33-40
Fertilized					
Sucrose, %	17.2	17.8	17.7	16.5	15.0
NO_3-N, p.p.m.	1139	846	933	2699	13039
Weight, lbs.	2.08	2.02	1.88	1.84	1.93
Non-fertilized					
Sucrose, %	17.4	18.1	17.8	17.6	16.5
NO_3-N, p.p.m.	497	460	526	670	4779
Weight, lbs.	1.36	1.18	1.10	1.35	1.61

These findings have a very practical application to the production of beet sugar and the processing of sugar from beets. It seems that the percentage sucrose is not greatly reduced in the root when the parts per million of NO_3-N in the petioles is less than 1000 but is reduced when that amount is exceeded. This finding agrees with those of Ulrich (16). On the fertilized plots an increase of parts per million of NO_3-N in the petioles above 1139 did not result in an increase in weight per root. Further, group 33 to 40 in the non-fertilized plots with 4779 parts per million of NO_3-N did not have as great weight per root as did the first three replication groups of the fertilized plots which had less than 1200 parts per million of NO_3-N in the petioles. This may have been due to a deficiency of P_2O_5 on the non-fertilized plots.

The means for the first order interaction of populations $\times$ treatments are listed in Table 7. This first order interaction is significant at the one percent level for percentage sucrose and weight per root and at the five percent level for parts per million of NO_3-N in the petioles.

The interaction populations $\times$ treatments is particularly interesting for percentage sucrose. Populations A54-1, A54-1BB, and 50-406 on the fertilized plots have materially lower percentage sucrose than they do on the non-fertilized plots, whereas there are no material reductions on the fertilized plots as compared with non-fertilized plots for populations 50-406BB, F_1 hybrid, and 52-307. This is particularly true of the last two populations.

The F_1 hybrid shows decided heterosis for percentage sucrose on the fertilized plots, whereas on the non-fertilized plots the

Table 7.—Means of Percentage Sucrose, Parts Per Million NO_3-N in the Petioles, and Weight Per Root for the Interaction of Populations X Treatments.

Treatment and Character	Population					
	A54-1	A54-1BB	50-406BB	50-406	F_1 Hybrid	52-307
Fertilized						
Sucrose, %	16.8	16.7	17.3	16.1	17.6	16.6
NO_3-N, p.p.m.	4233	4885	4267	2297	3060	3645
Weight, lbs.	2.60	2.64	2.04	1.02	2.23	1.16
Non-fertilized						
Sucrose, %	17.9	17.8	17.6	17.4	17.6	16.5
NO_3-N, p.p.m.	1736	1592	1491	962	1284	1252
Weight, lbs.	1.93	1.71	1.40	0.75	1.54	0.58

F_1 hybrid is not significantly higher in percentage sucrose than the inbred parent 50-406.

The first order interaction of populations × treatments for NO_3-N is illustrated by comparing populations A54-1BB and 50-406 for the two fertilizer treatments. The difference between treatments for A54-1BB is 3293 parts per million of NO_3-N and for 50-406 is 1335. Likewise, a comparison involving these same two populations and treatments illustrates the interaction for weight per root. The difference involving A54-1BB is 0.93 pound per beet and that involving 50-406 is 0.27 pound per beet.

Second order interactions

The second order interaction of biological interest in this study and the only one that will be discussed is replications × populations × treatments. The means for percentage sucrose, parts per million of NO_3-N in the petioles, and weight per root for this interaction are listed in Table 8.

The interaction, replications × populations × treatments, is significant at the one percent level for percentage sucrose and weight per root (see Table 2). The design of the experiment is not such as to provide an F value for testing the significance of this interaction for parts per million of NO_3-N in the petioles. However, the first order interactions of replications × treatments and populations × treatments were statistically significant at the one percent and five percent levels, respectively. The nature of the second order interaction for both percentage sucrose and weight per root is of economic importance. Something of the nature of the interaction involving percentage sucrose can be learned by the comparisons involving the different populations.

Table 8.—Means of Percentage Sucrose, Parts Per Million NO_3-N in the Petioles, and Weight Per Root for the Interaction of Replications X Populations X Treatments.

Population and Character	Replication Groups, Fertilized					Replication Groups, Non-Fertilized				
	1-8	9-16	17-24	25-32	33-40	1-8	9-16	17-24	25-32	33-40
A54-1										
Sucrose, %	17.1	17.6	17.7	16.8	14.6	18.0	18.4	18.3	18.2	16.6
NO_3-N, p.p.m.	1724	1350	829	3484	13778	671	452	640	864	6055
Weight, lbs.	2.90	2.55	2.41	2.44	2.69	1.93	1.66	1.61	2.02	2.43
A54-1BB										
Sucrose, %	16.9	18.2	17.9	16.2	14.5	17.8	18.7	18.3	17.5	17.0
NO_3-N, p.p.m.	1505	1154	1264	5368	15132	499	702	702	826	5231
Weight, lbs.	2.85	2.57	2.51	2.66	2.61	1.82	1.51	1.47	1.62	2.13
50-406BB										
Sucrose, %	17.6	18.1	18.1	17.0	15.5	17.4	18.0	17.9	17.7	16.8
NO_3-N, p.p.m.	1482	1050	1357	2656	14791	500	406	554	569	5426
Weight, lbs.	2.09	2.24	2.07	1.82	1.96	1.44	1.43	1.20	1.35	1.58
50-406										
Sucrose, %	16.8	16.8	16.6	15.6	14.7	17.9	17.8	17.7	17.3	16.4
NO_3-N, p.p.m.	702	551	632	788	8812	530	436	359	538	2948
Weight, lbs.	1.11	1.09	0.98	0.96	0.98	0.79	0.61	0.68	0.79	0.87
F_1 Hybrid										
Sucrose, %	18.2	18.5	18.2	17.0	16.0	17.6	18.3	17.7	17.6	16.8
NO_3-N, p.p.m.	852	390	648	2082	11328	234	374	524	398	4890
Weight, lbs.	2.29	2.49	2.19	2.03	2.16	1.60	1.39	1.20	1.67	1.82
52-307										
Sucrose, %	16.6	17 4	17.6	16.4	14.9	15.7	17.3	16.6	17.4	15.6
NO_3-N, p.p.m.	570	578	866	1817	14392	546	390	374	826	4126
Weight, lbs.	1.21	1.18	1.10	1.10	1.19	0.58	0.45	0.41	0.67	0.81

A study of Table 8 reveals that for all five replication groups the percentage sucrose of the F_1 hybrid exceeds that of A54-1 on the fertilized plots while the reverse is true (excepting the 33 to 40 group) on the non-fertilized plots. For the first three groups 50-406BB, the F_1 hybrid, and 52-307 show an increase in percentage sucrose on the fertilized plots as compared with the non-fertilized plots; whereas the reverse is true for populations A54-1, A54-1BB, and 50-406.

The parts per million of NO_3-N in the petioles involving the above comparisons are of interest. On the non-fertilized plots A54-1 has an average of 588 parts per million of NO_3-N in the petioles for the first three groups and the average percent sucrose is 18.2. The same values of the F_1 hybrid for the first three groups on the fertilized plots are 630 and 18.3. Apparently the F_1 hybrid and A54-1 have the same optimum concentration of nitrogen in the petioles for maximum percentage sucrose in the roots. However, the F_1 hybrid reaches this optimum at the high fertility level, whereas A54-1 reaches approximately this same concentration of NO_3-N at the lower fertility level. It seems that either A54-1 is more efficient in taking up nitrogen at the lower fertility and retains it in the petioles, or at the higher fertility the F_1 uses more nitrogen in metabolism or does not retain it in the petioles. This difference in reaction of populations may have a decided bearing on breeding varieties and hybrids better adapted to sugar production at higher fertility levels.

Another comparison involving 50-406BB with A54-1BB and A54-1 for the first three groups and the fertilized and non-fertilized treatments is of interest. An average increase in NO_3-N in the petioles from 486 parts per million on the non-fertilized plots of 50-406BB to 1296 on the fertilized was not accompanied by a decrease in percentage sucrose 17.8 to 17.9, whereas for A54-1BB and A 54-1 the corresponding values are 634 to 1308 accompanied by sucrose values of 18.3 to 17.7 and 588 to 1301 accompanied by sucrose values of 18.2 to 17.5. These results indicate that certain populations may be able to tolerate more NO_3-N in the petioles than others without an accompanying reduction in percentage sucrose.

Finally, the second order interaction of replications $\times$ populations $\times$ treatments is of interest in connection with information it furnishes concerning the possible nature of heterosis in this hybrid. Both the F_1 hybrid and the inbred parent 52-307 on the fertilized plots produced higher percentage sucrose for the first three replication groups than they did for these same

replication groups on the non-fertilized plots. The reverse is true for 50-406 as regards these same replication groups. The percentage sucrose for both the F_1 hybrid and 52-307 is less on the fertilized plots than on the non-fertilized plots for the last two replication groups. Thus the behavior pattern for the F_1 and 52-307 is the same, as regards the ability to produce higher percentage sucrose at the higher level of soil fertility. Hence, this ability to produce high percentage sucrose at the higher fertility level is partially or completely dominant. On the other hand the 50-406 inbred potentially is the higher percentage sucrose parent. This is shown by a comparison of 50-406 and 52-307 on the non-fertilized plots. The ability of 50-406 to produce a high percentage of sucrose is at least partially if not completely dominant in the F_1 hybrid. The ability of the F_1 hybrid to react as the inbred parent 50-406 in respect to high potential percentage sucrose production and as the 52-307 parent at the higher fertility level results in the heterosis of the F_1 hybrid grown on the high fertility plots. That is, the F_1 exceeds either parent in percentage sucrose on the fertilized plots.

Further study of the percentage sucrose values of Table 8 reveals that the behavior pattern of 50-406BB as compared with 50-406 on the fertilized and non-fertilized plots is very similar to the behavior pattern of the F_1 as compared with 50-406. The populations 50-406 and 50-406BB differ from each other in that the seed producing the plants of 50-406BB came from mother beet plants of 50-406 which at the time of flowering were exposed to pollen from 22 other varieties, strains, or inbreds. This evidence is important because it lends support to the finding that heterosis for percentage sucrose exists and indicates that it is not of too rare occurrence in sugar beets.

Another comparison of interest involves the relation between these three characters in replication group 1 to 8 and replication group 33 to 40. As can be determined from a study of Table 8 for all six populations on the fertilized plots there is a decrease in both percentage sucrose and weight per root of group 33 to 40 compared with group 1 to 8. There is a decided increase in parts per million of nitrate nitrogen in the petioles of group 33 to 40 as compared with group 1 to 8. Under conditions of this experiment the application of excesses of nitrogen results in a decided reduction of percentage sucrose and a slight reduction in weight per root.

Variances

Analyses of variance of the within-plot variances

The analyses of variance of the within plot variances for percentage sucrose and weight per root are given in Table 9.

Table 9.—Analyses of Variance of the Within Plot Variances for Percentage Sucrose and Weight Per Root.

Source of Variation	Mean Square		D. F.[1]	F Value		F Value at Level of	
	Sucrose	Weight		Sucrose	Weight	1%	5%
Replications	2.5861	0.1012	39	1.04	1.24	1.69	1.45
Populations	30.1922	4.8517	5	15.86*	77.63*	3.11	2.26
Treatments	9.3921	4.5036	1	3.15*	46.29*	7.31	4.08
R X P	1.9032	0.0625	195			1.39	1.26
R X T	2.9784	0.0973	39	1.20	1.19	1.69	1.45
P X T	4.0867	0.3171	5	1.64	3.88	3.11	2.26
R X P X T	2.4915	0.0818	195				

[1] D. F. designates degrees of freedom.

* The smaller mean square used in calculating these F values was that for R X P for populations and R X T for treatments; in all other cases the smaller mean square used in calculating F was R X P X T.

Whether there are significant differences for main effects can be determined by comparing the F values in columns 5 and 6 with those in columns 7 and 8.

For percentage sucrose the only significant differences are between populations. None of the interactions have F values that are significant. Providing there are not other complicating factors this lack of significant interactions justifies the use of the variances of the non-segregating populations to measure the environmental variability. These non-segregating populations are the two inbred lines, 50-406, 52-307, and the F_1 hybrid between them. It will be shown later that the two inbred lines show a larger variance for percentage sucrose than might have been expected. One explanation for the significant F values for populations is that they differ in amount of genetic variability.

For weight of root the F values for populations, treatments, and populations $\times$ treatments are statistically significant. This indicates that information of biological importance may be revealed by a more detailed study of the variances.

Main effects

The within plot variances and residual variances of percentage sucrose for main effects are listed in Table 10. The residual variances are obtained by subtracting the within plot variances of the F_1 hybrid from those of the other populations. The F values for testing whether residual variances differ significantly from zero are obtained by using the F_1 hybrid variance as the divisor and any respective population variance as the dividend.

Table 10.—Within Plot Obtained and Residual Variances of Percentage Sucrose and Weight Per Root in Pounds for Main Effects.

Population	Percentage Sucrose[1]		Weight Per Root in Pounds[2]		
	Obtained	Residual	Obtained	Estimated	Residual
A54-1	1.7852	0.8784	0.7052	0.3426	0.3626
A54-1BB	2.8303	1.9235	0.5795	0.3289	0.2506
50-406BB	1.9560	1.0492	0.3156	0.2502	0.0654
50-406	1.5143	0.6075	0.1087	0.1082	0.0005
F_1 hybrid	0.9068		0.2757	0.2789	—0.0032
52-307	1.6451	0.7383	0.1060	0.1047	0.0013

[1] The degrees of freedom for the obtained variances are 560. In any comparison the variance of the F_1 hybrid is used as the smaller mean square. It is also subtracted from the other variances to get the residual variances. The F values for the 1% and 5% levels are 1.24 and 1.16, respectively.

[2] The test used to determine whether the residual variances are significantly different from zero is that given by Powers, Robertson, and Remmenga (13).

All of the F values for the residual variances of percentage sucrose are greater than 1.24. Since this is true for the two inbred lines 50-406 and 52-307 the question arises whether there is considerable genetic variability between plants within these inbred lines. If such were the case one would expect the variance of the F_1 population to be greater. The residual variances of the A54-1, A54-1BB, and 50-406BB populations indicate considerable genetic variability between plants of these populations. It is of importance to the plant breeder to know whether there are significant differences between these populations and, if so, which populations have the greater residual variances. Whether there are significant differences in residual variances of any two given populations can be determined by calculating the F value for their within plot variances. Thus, for A54-1 and A54-1BB, F equals 2.8303 ÷ 1.7852 or 1.59. Each variance has 560 degrees of freedom and the F value for the one percent level of significance is 1.24.

It will be remembered that A54-1BB differs from A54-1 in that the mother beets giving rise to the seed that produced A54-1BB were exposed to pollen from 22 other populations, whereas A54-1 was exposed to only pollen of beets within the A54-1 population. Apparently A54-1BB has greater genetic variability than the female parent A54-1. Hence if the mean percentages of sucrose of these two populations are approximately the same or that of A54-1BB is the larger, the broad genetic base A54-1 should be the better population for making selections with which to start a polycross, recurrent selection, reciprocal

recurrent selection, or inbreeding program for the improvement of percentage sucrose.

Likewise, the residual variance of 50-406BB for percentage sucrose was significantly greater than that for 50-406. Again the broad base material has greater genetic variability. From Table 4 it can be seen that the mean percentage sucrose for 50-406BB is greater than that of 50-406. These facts indicate that for isolating a strain that would have superior combining ability when crossed with 50-406 at least some of the populations used as the pollen parent would provide desirable material for use in a recurrent selection breeding program.

The within plot mean variances for weight of root for main effects are listed in Table 10. The only residual variances significantly different from zero are those for A54-1, A54-1BB, and 50-406BB. In order to ascertain that the residual variance for 50-406BB is significant, methods given by Powers, Robertson, and Remmenga (13) can be employed. Since the means (2.26 lbs. and 2.18 lbs.) for A54-1 and A54-1BB are so nearly of the same magnitude the F test can be used to determine whether the variance of A54-1 is significantly greater than that of A54-1BB. The value of F obtained is 1.22. Each of these variances has 560 degrees of freedom, and the F value at the one percent level is 1.24 and at the five percent level is 1.16. It seems that the obtained variance of A54-1 for weight per root in pounds is greater than that of A54-1BB. It will be recalled that for percentage sucrose the within-plot obtained variance of A54-1BB was considerably greater than that of A54-1.

First order interactions

The within-plot mean variances and residual variances of percentage sucrose and the within-plot obtained mean variances, estimated and residual mean variances of weight per root in pounds for the interaction of populations $\times$ treatments are given in Table 11. The variances for percentage sucrose will be considered first.

Again the F_1 hybrid variance is used as the smaller mean square in calculating F and the smaller variance in estimating the residual variance. The difference between the F_1 hybrid variances on the fertilized and non-fertilized plots is not significant at the five percent level. In testing significance the degrees of freedom of all variances for percentage sucrose are 280.

Again the residual variances for percentage sucrose on both the fertilized and non-fertilized plots differ significantly from 0 for all populations.

Table 11.—Within-Plot Obtained Variances and Residual Variances of Percentage Sucrose and Within-Plot Obtained Variances, Estimated and Residual Variances of Weight Per Root in Pounds for the Interaction of Populations X Treatments.

Population	Percentage Sucrose[1]		Weight Per Root in Pounds[2]		
	Obtained	Residual	Obtained	Estimated	Residual
Fertilized					
A54-1	1.6555	0.7378	0.8691	0.4007	0.4684
A54-1BB	2.4474	1.5297	0.7640	0.4076	0.3564
50-406BB	1.8959	0.9782	0.4033	0.3049	0.0984
50-406	1.6652	0.7475	0.1398	0.1282	0.0116
F_1 hybrid	0.9177		0.3370	0.3386	—0.0016
52-307	1.1952	0.2775	0.1586	0.1535	0.0051
Non-fertilized					
A54-1	1.9150	1.0190	0.5412	0.2861	0.2551
A54-1BB	3.2132	2.3172	0.3950	0.2485	0.1465
50-406BB	2.0160	1.1200	0.2279	0.1954	0.0325
50-406	1.3634	0.4674	0.0776	0.0869	—0.0093
F_1 hybrid	0.8960		0.2144	0.2208	—0.0064
52-307	2.0950	1.1990	0.0535	0.0562	—0.0027

[1] The degrees of freedom for the within plot obtained variances are 280. In any comparison the variance of the F_1 hybrid is used as the smaller mean square. The values of F at the 1% and 5% levels are 1.39 and 1.26, respectively. All residual variances for percentage sucrose with the exception of 52-307 on the fertilized plots are significant at the 1% level. The 52-307 residual variance on the fertilized plots is significant at the 5% level.

[2] The test used to determine whether the residual variances are significantly different from zero is that given by Powers, Robertson, and Remmenga (13).

Whether the residual variances for percentage sucrose of the inbreds 50-406 and 52-307 result from genetic variability within these populations is of interest. The smaller variance of the F_1 hybrid as compared with the variances of the two inbreds is not readily explained on the basis that residual variances of the inbreds are genetic. A possible explanation of the greater variances of the inbred is due to a greater response of these inbred plants to environmental changes. This could be caused by the reduced vigor of the inbred plants as compared with plants of the F_1 and other populations. A study of Table 7 reveals that the means of inbreds for weight per root are considerably less than the means for the other populations. Further, the decrease in weight per root in going from the fertilized plots to the non-fertilized plots is greater for 52-307 (1.16 to 0.58) than for 50-406 (1.02 to 0.75). This, together with the fact (Table 11) that 52-307 shows a significant increase in the magnitude of the variance for percentage sucrose on the non-fertilized plots as compared with the fertilized plots whereas 50-406 does not, lends some support to the deduction that increased variability of the inbred plants over the F_1 plants may be due to a greater response to environmental changes by the inbred plants and such response

in turn is due to reduced vigor. If this is the explanation 50-406 which has the smaller weight per root on the fertilized plots should have a larger variance on these plots and 52-307 which has the smaller weight per root on the non-fertilized plots should have the greater variance on these plots. Such is the case and the differences are significant at the one percent level. On the other hand the variances for percentage sucrose of 50-406 are not significantly different at the two fertility levels even though the mean weight per root of this inbred is significantly less at the lower fertility level. The evidence as a whole seems to indicate that genetic variability is playing very little part in the increased variability for percentage sucrose of the inbreds as compared with their F_1 hybrid. This is supported by previous studies with 52-307 in which the plants were spaced to avoid competition between plants. In this previous experiment (see Powers, 9) there was no evidence of genetic variability between plants within inbred line 52-307.

It is believed that the increased variability for percentage sucrose of populations A54-1, A54-1BB, and 50-406BB is due mostly to genotypic differences between plants and the conventional interactions between genotypes and the environment. By conventional interactions between genotypes and environment are meant those ordinarily encountered in genetic studies and not those produced as a result of plants of a comparatively homozygous population having a greater response in range to environmental changes than do plants of another homozygous population.

The within plot obtained mean variances, estimated and residual variances of weight per root in pounds for the interaction of populations $\times$ treatments are listed in Table 11. On the fertilized plots and non-fertilized plots the residual variances are significantly different from zero for A54-1, A54-1BB, and 50-406BB. For methods of testing significance see Powers, Robertson, and Remmenga (13). The two inbred lines and the F_1 hybrid do not have any residual variances that are significant at the five percent level. Hence, there is no evidence of genetic variability among the plants within either of the inbred lines or among plants within the F_1 hybrid population. There is rather conclusive evidence for considerable genetic variability among the plants of populations A54-1 and among plants of A54-1BB for weight per root. Some genetic variability is occurring among the plants of 50-406BB.

These findings concerning genetic variability for percentage sucrose and weight per root indicate that a study of the frequency distributions would provide important biological information.

Frequency Distributions

The obtained and calculated frequency distributions and differences and proportions for percentage sucrose on the fertilized and non-fertilized plots are listed in Table 12 for populations A54-1 and A54-1BB. The study of the frequency distributions in this article is limited to those of these two populations. They show decided genetic variability and hence are of most interest from the standpoint of plant breeding. For the detailed frequency distributions for all populations see Powers, et al (12) and for details of methods of analyses and tests of significance see Powers, Locke, and Garrett (11), Powers (9), and Powers, et al (12).

The data in Table 12 fall into three rather well defined groups of individuals which have been termed genetically inferior, genetically mediocre, and genetically superior. The estimated numbers and proportions of the first and last groups are listed for each class and population. Also the last two columns give the total numbers and the proportions. If a population is heterozygous, heterogeneous, or both, genetically inferior and genetically superior individuals would be expected. A study of Table 12 reveals that both types are occurring in both populations and both treatments with the possible exception of genetically-superior individuals in population A54-1 on the fertilized plots. The odds are not great that the value 12, for A54-1 listed opposite difference and under total genetically superior, is significantly different from zero. The corresponding value of 21 for A54-1 on the non-fertilized plots is significantly different from zero. An examination of Table 12 shows that no genetically-superior individuals of A54-1 are expected in the last three classes on the fertilized plots, whereas on the non-fertilized plots 10 such individuals are expected among a total of 41. These results indicate that for percentage sucrose it would be much easier to select genetically-superior individuals from the non-fertilized plots than from the fertilized plots. The same trend is noted for A54-1BB but it is much less marked. It cannot be overlooked that for both populations for the non-fertilized plots the estimated proportion of genetically-superior individuals is highest in the last two classes.

In the last three classes the proportions of genetically-superior individuals are higher for A54-1BB than for A54-1 on both the fertilized and non-fertilized plots. These differences are greater than would be expected by chance.

The proportion of genetically-inferior individuals does not differ greatly for populations and treatments. The populations

Table 12.—Obtained and Calculated Frequency Distributions and Differences and Proportions for Percentage Sucrose, Fertilized and Non-Fertilized plots.

Treatment, Population and Distribution	Upper Limit of Class, Percent Sucrose															Total Genetically	
	0 to 11.25	12.00	12.75	13.50	14.25	15.00	15.75	16.50	17.25	18.00	18.75	19.50	20.25	21.00	21.75 and over	Inferior	Superior
Fertilized	No.	No.	No.	No.	No.	No.	No.	No.	No.	No.	No.	No.	No.	No.	No.	No.	No.
A54-1																	
Obtained	3	4	1	9	18	15	23	51	60	64	36	25	9	1	1	35	136
Calculated	0	0	1	4	10	23	41	57	60	54	37	20	9	3	1	15	124
Difference	3	4	0	5	8					10	—1	5	0	—2	0	20	12
Proportion	1.00	1.00		0.56	0.44					0.16		0.20				0.57	0.09
A54-1BB																	
Obtained	6	4	5	7	20	20	37	37	32	54	49	30	11	6	2	42	152
Calculated	0	0	2	4	12	26	42	58	62	51	34	18	8	2	1	18	114
Difference	6	4	3	3	8					3	15	12	3	4	1	24	38
Proportion	1.00	1.00	0.60	0.43	0.40					0.06	0.31	0.40	0.27	0.67	0.50	0.57	0.25
Non-fertilized																	
A54-1																	
Obtained	3	1		1	4	12	11	25	36	62	66	58	26	11	4	32	99
Calculated	0	0		0	0	3	10	28	56	74	71	47	22	7	2	13	78
Difference	3	1		1	4	9	1					11	4	4	2	19	21
Proportion	1.00	1.00		1.00	1.00	0.75	0.09					0.19	0.15	0.36	0.50	0.59	0.21
A54-1BB																	
Obtained	1	3	2	4	8	9	13	24	42	61	38	62	30	17	6	40	115
Calculated	0	0	0	0	1	3	12	32	57	76	69	44	19	6	1	16	70
Difference	1	3	2	4	7	6	1					18	11	11	5	24	45
Proportion	1.00	1.00	1.00	1.00	0.88	0.67	0.08					0.29	0.37	0.65	0.83	0.60	0.39

do not differ materially within a treatment. However there is a significantly greater proportion of genetically-inferior individuals in the lower two classes of the frequency distribution on the fertilized plots. Selection of individuals in the lower two classes of the frequency distribution would be expected to result in only genetically-inferior individuals. These are termed the identifiable-genetically-inferior individuals, as the lower two classes do not have any expected chance deviates. On the non-fertilized plots this is true of the lower four classes. Hence, there are definite differences between treatments.

It is interesting that there are no identifiable-genetically-superior individuals for percentage sucrose (Table 12) either on the fertilized or non-fertilized plots. That is, some chance deviates occur in all classes. To identify the genetically-superior individuals a progeny test is required. However as noted above there is a difference between populations and treatments in the proportion of genetic deviates to chance deviates for percentage sucrose in the more desirable classes. However, since this study has shown that there are decided interactions between populations and treatments it is not advisable to conduct the breeding program at the lower fertility level if the resultant varieties or hybrids are to be grown at higher fertility levels.

The obtained and calculated frequency distributions and differences and proportions for weight per root on the fertilized and non-fertilized plots are listed in Table 13.

On the fertilized plots there is no material difference between populations as to the proportion of genetically-superior individuals for weight per root. Also the number of identifiable-genetically-superior individuals is not significantly different. However, on the non-fertilized plots population A54-1 offers more promise than A54-1BB as the genetically-superior individuals occur in higher classes of the frequency distribution. Also, the number of identifiable-genetically-superior individuals is not significantly different for these two populations, but those of A54-1 occur in higher classes.

For weight of root there is only one identifiable-genetically-inferior individual and it occurs in population A54-1BB on the fertilized plots.

The data in Tables 12 and 13 for percentage sucrose and weight per root indicate that on the fertilized plots, when breeding for both characters, population A54-1BB would be superior to A54-1, whereas on the non-fertilized plots the reverse would

Table 13.—Obtained and Calculated Frequency Distributions and Differences and Proportions for Weight Per Root, Fertilized and Non-Fertilized Plots.

Treatment, Population and Distribution	Upper Limit of Class, Pounds											Total Genetically	
	0 to 0.5	1.0	1.5	2.0	2.5	3.0	3.5	4.0	4.5	5.0	5.5 and over	Inferior	Superior
Fertilized	No.	No.	No.	No.	No.	No.	No.	No.	No.	No.	No.	No.	No.
A54-1													
Obtained	4	9	20	59	60	66	49	29	11	10	3	92	53
Calculated	1	3	16	44	78	86	59	25	7	1	0	64	33
Difference	3	6	4	15				4	4	9	3	28	20
Proportion	0.75	0.67	0.20	0.25				0.14	0.36	0.90	1.00	0.30	0.38
A54-1BB													
Obtained	1	4	31	41	83	48	58	30	16	5	3	36	54
Calculated	0	3	14	42	76	85	62	28	8	2	0	17	38
Difference	1	1	17					2	8	3	3	19	16
Proportion	1.00	0.25	0.55					0.07	0.50	0.60	1.00	0.53	0.30
Non-fertilized													
A54-1													
Obtained	8	35	56	80	72	38	19	9	2		1	43	31
Calculated	3	17	57	99	90	42	10	2	0		0	20	12
Difference	5	18					9	7	2		1	23	19
Proportion	0.62	0.51					0.47	0.78	1.00		1.00	0.53	0.61
A54-1BB													
Obtained	9	39	83	93	53	31	9	1	2			131	43
Calculated	5	28	81	109	71	22	4	0	0			114	26
Difference	4	11	2			9	5	1	2			17	17
Proportion	0.44	0.28	0.02			0.29	0.56	1.00	1.00			0.13	0.40

be true. To determine whether such is the case the more desirable classes of the frequency distribution for both characters are studied.

The culture numbers and values for those individual roots of A54-1 and A54-1BB that exceeded 17.25 percent sucrose and 3.5 pounds on the fertilized plots and that exceeded 17.25 percent sucrose and 3.0 pounds on the non-fertilized plots are listed in Table 14. In the second from the last row of each fertilizer treatment are listed the root means and in the last row are listed the population means. The total number of individuals in any given population within a fertilizer treatment is 320. The percentage sucrose and weight for any given root of Table 14 correspond. For example, the percent sucrose and weight per root of root number 1 of population A54-1 on the fertilized plots are 17.4 percent and 4.12 pounds as shown in Table 14.

Table 14.—Roots of A54-1 and A54-1BB from the Fertilized Plots that Exceeded 17.25 Percent Sucrose and 3.5 Pounds and Roots of the Same Populations from the Non-Fertilized Plots that Exceeded 17.25 Percent Sucrose and 3.0 Pounds.

Fertilized						Non-Fertilized					
Root No.		Sucrose		Weight		Root No.		Sucrose		Weight	
A54-1	A54-1 BB	A54-1	A54-1 BB	A54-1	A54-1 BB	A54-1	A54-1 BB	A54-1	A54-1 BB	A54-1	A54-1 BB
No.	No.	%	%	Lbs.	Lbs.	No.	No.	%	%	Lbs.	Lbs.
1	1	17.4	17.3	4.12	4.85	1	1	17.4	17.4	3.84	3.19
2	2	17.6	17.6	3.55	3.51	2	2	17.4	17.4	3.26	3.15
3	3	17.8	17.6	4.46	5.07	3	3	17.4	18.0	3.24	3.16
4	4	17.8	17.8	3.71	3.55	4	4	17.5	18.0	3.41	3.47
5	5	17.8	17.8	3.92	4.14	5	5	17.5	18.2	3.03	3.27
6	6	17.8	18.0	4.79	4.37	6	6	17.6	18.3	3.16	3.36
7	7	17.8	18.0	4.52	3.83	7	7	17.9	18.3	4.45	3.06
8	8	17.9	18.0	3.67	4.79	8		18.2		3.57	
9	9	18.3	18.0	4.23	4.08	9		18.2		3.14	
	10		18.0		3.71	10		18.6		3.56	
	11		18.3		3.68	11		18.7		3.07	
	12		18.4		3.58	12		19.2		3.17	
	13		18.6		4.17	13		19.3		3.83	
	14		18.7		5.20	14		19.4		3.06	
	15		18.8		3.55	15		19.5		3.11	
	16		19.0		4.23	16		19.8		3.21	
	17		19.0		4.16	17		20.1		3.15	
	18		19.2		3.91	18		20.8		3.36	
Mean		17.8	18.2	4.11	4.13			18.6	17.9	3.37	3.24
Population mean		16.8	16.7	2.60	2.64			17.9	17.9	1.93	1.71

A study of Table 14 reveals that on the fertilized plots there were nine roots of A54-1 which had more than 17.25 percent sucrose and weighed more than 3.5 pounds. There were 18 such roots for A54-1BB. The highest percent sucrose for any root of A54-1 was 18.3 and only one root reached this value. For population A54-1BB there was one root with 18.3 percent sucrose and seven roots which had higher values, the highest value being 19.2 percent sucrose. The highest weight per root for A54-1 was 4.79 pounds and for A54-1BB was 5.2 pounds. Three roots of A54-1BB had a value of 4.79 pounds or higher. These findings for the fertilized plots indicate that A54-1BB would be the more desirable population of the two from which to start a breeding program.

On the non-fertilized plots the number of roots of A54-1 having sucrose values greater than 17.25 percent and weighing more than 3.0 pounds was 18 and the corresponding number for A54-1BB was seven. The highest percent sucrose for any root of A54-1BB was 18.3 on the non-fertilized plots whereas nine roots of A54-1 grown on the non-fertilized plots exceeded this value of 18.3 percent. The greatest weight for any root of A54-1BB on the non-fertilized plots was 3.47 pounds. By adding to this the differential, 0.13 pounds, between the means of the two populations a value of 3.60 is obtained. There were three roots of A54-1 that exceeded 3.60 pounds. These findings for the non-fertilized plots indicate the reverse of that found for the fertilized plots. In other words A54-1 instead of population A54-1BB would be expected to be the more desirable population for starting a breeding program.

Further, the data of Table 14 indicate a decided interaction between populations and fertilizer treatments in regard to the number of individuals falling in the group from which desirable selections might be made. This might be expected from the analyses of variance for percentage sucrose and weight per root given in Table 2. In this table the interaction of populations $\times$ treatments is significant at the one percent level.

It is of importance to determine whether this difference noted for populations in the proportion of desirable individuals at the two fertility levels is statistically significant. Homogeneity chi square is used to test how frequently such results would be expected by chance. In the data of Table 15 there are three degrees of freedom for homogeneity chi square. These degrees of freedom are populations 1, treatments 1, and populations $\times$ treatments 1. The population chi square is calculated from the row totals given in the last two columns of Table 15; treatment

chi square is calculated from the column totals given in the last row of Table 15. The total chi square is calculated from the data within populations and treatments, and the interaction chi square is calculated by subtracting population chi square and treatment chi square from total chi square. The proportion from which the homogeneity chi squares are calculated is obtained from the grand total. For example the grand total is 1280. The proportion in class 1 is $1228 \div 1280 = 0.959375$ and $52 \div 1280 = 0.040625$. The theoretical for both populations and treatments is $0.959375 \times 640 = 614$ and $0.040625 \times 640 = 26$. Hence the chi square for both populations and treatments is $[(1)^2 \div 614$ plus $(1)^2 \div 26]2 = (0.001628 + 0.038461)\,2 = 0.080178$.

Table 15.—The Number of Roots Listed in Table 14 Having a High Weight of Root and a High Percentage Sucrose Compared with the Balance of the Population; for Populations A54-1 and A54-1BB and for the Fertilized and the Non-Fertilized Plots.

	Fertilized		Non-Fertilized		Total	
	Weight, Lbs. and Sucrose, %		Weight, Lbs. and Sucrose, %		Weight, Lbs. and Sucrose, %	
	0.5-3.0 9.75-17.25	3.6-5.5 17.26-22.50	0.5-3.0 9.75-17.25	3.1-5.5 17.26-22.50	Class	
Population	(Class 1)	(Class 2)	(Class 1)	(Class 2)	1	2
	No.	No.	No.	No.	No.	No.
A54-1	311	9	302	18	613	27
A54-1BB	302	18	313	7	615	25
Total	613	27	615	25	1228	52

Total homogeneity chi square is calculated as follows. The theoretical expected is 0.959375×320 and 0.040625×320 for classes 1 and 2, respectively. Completing the calculations gives 307 for class 1 and 13 for class 2. Chi square $= 0.052117 + 1.230769 + 0.081433 + 1.923077 + 0.081433 + 1.923077 + 0.117264 + 2.769231 = 8.178401$. The interaction chi square is $8.178401 - (0.080178 + 0.080178) = 8.018045$. The value of P for both populations and treatments lies between 0.80 and 0.70. The value of P for the interaction chi square lies between 0.01 and one minus infinity.

The fact that the interaction chi square has a P value lying between 0.01 and one minus infinity is rather convincing evidence that the relation between populations as to the proportions of individuals in the more desirable class (2) is not the same for the two fertilizer treatments. The nature of this interaction or relation between populations for the two fertilizer treatments is important agronomically. It can be calculated from the data of Table 15 that for population A54-1 on the fertilized plots the percent of

individuals in class 2 was 2.8 whereas for A54-1BB the corresponding value was 5.6. On the non-fertilized plots the situation was reversed, A54-1 having 5.6 percent of the individuals occurring in class 2 and A54-1BB having 2.2 percent of the individuals falling in this class. These results indicate that on the fertilized plots a greater proportion of the selections from A54-1BB would have both higher sucrose and greater weight per root than do the selections from A54-1 and that on the non-fertilized plots the reverse is true.

It will be remembered from a discussion of Table 14 that not only were there a greater number of individuals of A54-1BB in the desirable class on the fertilized plots but that some of these individuals had a higher percent sucrose than did any of the individuals of population A54-1. Also this latter was true for weight per root. Since the means of the two populations, A54-1 and A54-1BB, were essentially the same, 16.8 and 16.7 for percent sucrose and 2.60 and 2.64 pounds for weight per root, respectively (see Table 14), it seems that some of the individuals of A54-1BB must be genetically superior to the best individuals of population A54-1 for both percentage sucrose and weight per root. It must be kept in mind that this applies to the higher fertility level. As shown previously the reverse is true for the low fertility level. That is, at the low fertility level some of the individuals of A54-1 must be genetically superior to the best individuals of population A54-1BB for both characters.

Progeny Tests

Selections were made in the border rows of each plot of the populations and from a non-fertilized adjacent area. It will be remembered that these border rows were all planted to population A54-1. This was done so that such a selection experiment could be conducted. The series numbers, replications, and treatments are shown in Diagram 1.

This immediately adjacent non-fertilized area was also planted to A54-1. It was divided into 12 plots of 24 plants each, there being 40 such unit areas making potentially a total of 11,520 plants in this selection experiment at the low fertility level. A nearly perfect stand was obtained at the time of thinning. There were a few plants lost during the growing season. However, at time of selection there was an excellent stand. Only competitive roots were selected; that is, those beets which had beets on four sides of them. This was true of the selections made from the border rows of the experiment depicted in Diagram 1. The environmental variances calculated from the F_1 plants of the experiment and the inbreds were used to identify those individuals for

which the odds were greatest that they would be genetically-superior. For weight of root 30 plants were selected from each unit of 12 plots on the basis of observation as having the greatest size. This made a total of 1200 roots thus selected (40×30). These were trimmed as mother beets and each weighed and sucrose determinations made. Then on the basis of the predicted environmental variances for weight of root and the mean of A54-1 for each unit for both weight of root and percentage sucrose these 1200 roots were reduced to 400 which were stored in the root cellar. Later these were further selected to only 32 roots and one-half of each root was grown as a mother beet in the greenhouse during the winter of 1956-57. The other half was divided into two quarters and grown vegetatively (see Powers, Finkner, Doxtator, and Swink, 10). The procedures and formula used in identifying those individuals for which the odds are greatest that they are genetically superior for both percentage sucrose and weight of root are given by Powers (9) and Powers, et al (12).

During the entire period of flowering and dehiscence, pollen was collected from all of the 32 plants and applied to the non-bagged flowers of each plant. The apparatus used in collecting and dispensing the pollen is described by Krouch, Kintzley, and Taylor (5). Seed was saved from each of the 32 mother beets of A54-1, and grown in the polycross test in the field in 1957.

The design of the experiment was very similar to that given by Powers (9) and Powers, Finkner, Doxtator, and Swink (10). The individual progenies of the 32 selections were divided into three blocks composed of 10 plots plus two plots of A54-1 for blocks 1 and 2, and 12 plots plus two plots of A54-1 for block 3. The progenies with the two check plots of A54-1 were randomized within blocks and the blocks were randomized within replications. There were five replications. The design differs from that described by Powers, Finkner, Doxtator, and Swink (10) in that the same progenies occur in the same block in all replications. The material was grown at a high fertility level, 100 lbs. P_2O_5 and 200 lbs. N per acre, 100 lbs. of N being applied before planting and another 100 lbs. after thinning on June 27.

Before presenting the data it seems well to consider the fundamental information that the polycross test might contribute. First it should provide information as to whether it is possible to isolate any of the genetically-superior individuals by the methods described by Powers (9) and Powers, et al (12). Also, since the polycross method tests for general combining ability it should provide information as to whether these genetically-

superior individuals have general combining ability. If genetically-superior individuals do not have general combining ability, failure to disclose genetically-superior individuals may be due to the test employed. Hence, it follows that if any are found by the polycross progeny test they would have general combining ability.

Percentage sucrose, weight of roots per plot, and weight of sugar per plot of the average of six A54-1 checks and progenies of 32 selections in the polycross test are listed in Table 16. The 32 progenies average the same in percentage sucrose as the A54-1 population from which they were selected. The increase in weight of root and weight of sugar per plot was 7.1 percent. The odds are considerably greater than 99:1 against this increase of 7.1 percent being due to chance. This increase in weight of root per plot has been obtained without any decrease in percentage sucrose. This raises the question as to whether any of the progenies represent both an increase in percentage sucrose and weight of root per plot.

Table 16.—Percentage Sucrose, Weight of Roots Per Plot, and Weight of Sugar Per Plot of Average of Six A54-1 Checks and Progenies of 32 Selections in the Polycross Test, the Original Selections Being from A54-1 Grown on Non-Fertilized Plots in 1956.

Selection and Character	Replication					Mean	Percent of Check
	1	2	3	4	5		
A54-1, check							
Percentage sucrose	13.9	15.2	15.7	15.2	15.4	15.1	
Weight of roots, lbs.	39.33	35.46	38.42	37.05	37.53	37.56	
Weight of sugar, lbs.	5.47	5.39	6.03	5.59	5.79	5.66	
32 progenies							
Percentage sucrose	14.0	15.1	15.4	15.5	15.5	15.1	100.0
Weight of roots, lbs.	42.18	40.39	39.88	39.05	39.58	40.22	107.1
Weight of sugar, lbs.	5.90	6.11	6.11	6.03	6.14	6.06	107.1

In Table 17 are listed percentages of sucrose, weight of roots per plot, and weight of sugar per plot for the average of two A54-1 checks and for two progenies of selections in the polycross test. In all five replications the percentage sucrose for the progenies of selections 2W-37 and 4W-34 is greater than the average of the two checks of A54-1. The odds against these being chance deviations (taken individually) are greater than 30 to 1 and that both should occur due to chance is rather unlikely. The odds against the increases noted for weight of root being due to

chance deviations from the check are even greater than that for percentage sucrose. It follows that increases in weight of sugar per plot of the two progenies over the population from which the mother beets were selected are not likely to be due to chance deviations. It seems highly probable that at least one of these two progenies represents both an increase in percentage sucrose and weight of roots per plot. The increase in weight of sugar per plot for the progeny of selection 4W-34 is 22.4 percent of the population from which the selections were made. At least it is apparent that increased weight of root has not been accompanied by a decrease in percentage sucrose.

Table 17.—Percentage Sucrose, Weight of Roots Per Plot, and Weight of Sugar Per Plot of Average of Two A54-1 Checks and Progenies of Two Selections in the Polycross Test, the Original Selections Being from A54-1 Grown on Non-Fertilized Plots in 1956.

Selection and Character	Replication					Mean	Percent of Check
	1	2	3	4	5		
A54-1, check							
Percentage sucrose	14.3	15.6	16.0	16.1	15.6	15.5	
Weight of roots, lbs.	41.37	34.80	37.36	33.22	35.92	36.53	
Weight of sugar, lbs.	5.92	5.42	5.96	5.35	5.64	5.66	
2W-37							
Percentage sucrose	15.8	15.8	16.2	16.4	16.6	16.2	104.5
Weight of roots, lbs.	44.92	35.35	41.92	37.28	34.20	38.73	106.0
Weight of sugar, lbs.	7.10	5.59	6.79	6.11	5.68	6.25	110.4
4W-34							
Percentage sucrose	14.4	16.3	16.3	16.9	15.8	16.0	103.2
Weight of roots, lbs.	45.25	48.35	45.32	40.77	37.88	43.51	119.1
Weight of sugar, lbs.	6.52	7.88	7.39	6.89	5.99	6.93	122.4

This increase of 22.4 percent can be attributed to the general combining ability of selection 4W-34. The data presented in Tables 16 and 17 furnish rather convincing evidence that the method outlined by Powers (9) and Powers, et al (12) for the identification and selection of genetically-superior individuals is effective. Hence by using this method of selecting genetically-superior individuals the number of progenies that it is necessary to test can be materially reduced in any of the breeding programs such as production of synthetic varieties, polycross method of breeding, recurrent selection, reciprocal recurrent selection, or the production of inbred lines for use in hybrids.

Ten of the more promising of the original 32 mother beets that were propagated asexually are being combined to produce a

synthetic variety. It remains to be determined whether such a synthetic variety will produce more sugar per acre and if so how much more. It will be interesting to see, if any gain is obtained, whether the gain will be attributable to both percentage sucrose and weight per root.

Discussion and Conclusions

The results and findings of the population genetic studies at different levels of soil fertility have considerable bearing on plant breeding programs for sugar beets and other crops. By making population genetic studies and applying the partitioning method of estimating the numbers and proportions of genetically-superior individuals the plant breeder can evaluate different populations for their breeding potential at different levels of soil fertility and determine the numbers and proportions of individuals expected to be genetically-superior. Also, in the process of evaluating populations the plant breeder obtains information as to what classes of the frequency distribution provide the greatest proportion of genetically-superior individuals. Hence he learns within what ranges of the character expression selection should be made, and, if a progeny test is being conducted, the number or proportion of the progeny that is expected to be genetically superior. This information allows the plant breeder to decide how many mother beets must be progeny tested to isolate the number of genetically-superior mother beets required to carry on the breeding program.

Also, the studies show that certain requirements should be met as regards the growing of the material in which selections are made (see Powers, 9, page 429). Further, certain procedures in making the selections should be followed if genetically-superior individuals are to be identified and isolated. Probably one of the most important requirements is that the selections be made within small areas which here have been termed units. The selections, the results of which are reported in this article, were made from 40 units. The size of units found by Powers (9) and by this study to be effective was 22 feet long by 20 feet wide and contained 288 plants. The 22 $\times$ 20 feet unit provides 12 rows with 24 plants per row. Two of these 12 rows are planted to non-segregating populations to provide an estimate of the environmental variability within the unit. The two rows are randomized within the unit. The environmental variance within units, but an average for all units, provides an estimate of the environmental variance. The square root of this variance provides an estimate of the environmental standard error. This standard error is used to determine the odds against any given individual being a chance

deviate from the mean used as the basis for selection. As the mean of the unit is the most accurate of any mean that can be calculated from the plants within the unit, it provides the best basis for selection. However, in some cases the plant breeder may desire to enter at random another population to be used as the basis for selection.

In the present study the mean of the population in which selections were being made was used as a basis of selection. The original population from which selections were made numbered approximately 11,520 individuals. The population in which selection was made was A54-1. The odds were good that 32 individuals were genetically-superior to the mean of population A54-1. To learn whether selection had been effective and whether these 32 individuals or some of them were genetically superior they were subjected to a polycross testing procedure (Tysdal, et al, 15). The method employed in obtaining seed for the polycross test is described by Powers, et al (10). The polycross test measures general combining ability. On an average the progenies of the 32 selected mother beets were superior to A54-1 in yield of roots per acre and equal in percentage sucrose. The evidence was rather conclusive in showing that probably two of the 32 progenies excelled in both yield of roots and percentage sucrose. This evidence substantiates the methods used in making the selections but leaves the plant breeder with the problem of how to utilize the general combining ability of these genetically-superior individuals saved as mother beets and asexually propagated.

Studies on percentage sucrose and weight per root indicate that heterosis for both these characters is common. Hence the mother beets identified as genetically-superior and isolated by selection from small areas and the polycross test are almost assuredly genetically-superior because of heterosis. The problem has resolved into one of determining how to take advantage of the heterosis exhibited by these mother beets.

To do this consideration needs to be given to genetic principles that may have a decided bearing on procedures. Visualizing an extreme situation and taking a specific example the 10 asexually propagated individuals making up the synthetic variety could be likened to F_1 hybrids genetically identical to each other. Such would be the situation if all 10 were derived from hybridization between two homozygous inbreds. In such an event the synthetic variety produced by interpollination of the 10 mother beets would be essentially an F_2 population and would have lost much of the advantage attributable to heterosis. The other extreme may be visualized as follows. Each of these 10 mother beets re-

sulted from the union of two gametes having high general combining ability, and, in turn, the 20 gametes involved would have combined well in all possible combinations. In such an event the synthetic variety produced by inter-pollination of the 10 mother beets would be expected to retain much of the genetic superiority attributable to heterosis. Probably the actual genotypes of the 10 mother beets are such that the behavior of the synthetic variety will be between the two extremes depicted above. The problem has resolved into one of determining how to utilize in a breeding program the genetic-superiority of selected mother beets.

As pointed out previously (Powers, 9) the methods of breeding most generally employed to utilize heterosis take advantage of either general combining ability or specific combining ability, or both. The polycross method of breeding (Tysdal, et al, 15) is well adapted to take advantage of general combining ability and is readily adapted to breeding sugar beets. By producing synthetic varieties from the genetically-superior individuals isolated, comparatively speaking, it offers a rapid method of improvement. The recurrent selection (Hull, 3) and the reciprocal recurrent selection methods (Comstock, et al, 1) are designed to take advantage of both general and specific combining ability. The inbred line method of breeding followed by hybridization is designed to take advantage of specific combining ability. The method of making selections from small units outlined in this and a previous article (Powers, 9) is designed, by isolating genetically-superior individuals, to reduce the great mass of material that otherwise it would be necessary to work with in using the polycross, recurrent selection, reciprocal recurrent selection, and inbred line methods of breeding. Hence, all of these breeding methods can and probably should be incorporated in one overall program. Those populations composed of genetically-superior individuals isolated by selection from small units and by a subsequent polycross test would be suited for one parent in recurrent selection, as one source in a reciprocal recurrent selection program, and for producing inbred lines. In turn, the selections from small units, the material resulting from the polycross method of breeding, the material resulting from the recurrent selection method of breeding, and the material resulting from the reciprocal recurrent selection method of breeding should provide excellent material for establishing inbred lines to be used in producing hybrids.

For example, at least some of the inbred lines established by the above methods of breeding in which selection was being

practiced to cumulate desirable genes should combine well with each other. The number of inbreds that it would be necessary to establish and carry to accomplish improvement should have been materially reduced by the selection practiced in the small units and by the subsequent polycross tests. Inbred lines developed from the source in which selection was being practiced to cumulate genes that combine well with a given inbred should combine well with that inbred. Likewise, inbreds produced from one source of the reciprocal recurrent selection breeding program should combine well with those of the opposite source. The number of inbred lines from the two sources in the reciprocal recurrent selection program that it would be necessary to establish and test for combining ability should not be great, probably not more than 10 from each source. This would be due to some extent to the fact that selection in small units and the polycross method of testing had been employed to establish the two sources used in the reciprocal recurrent selection program.

It should be fully realized and kept in mind that population genetic studies, identification of genetically-superior individuals, and applying the partitioning method of estimating the numbers and proportions of genetically-superior individuals in the desirable class ranges are integral and essential parts of the breeding program. Probably one of the most important functions of the methods and formulas presented in this and previous articles is to provide a means of evaluating the breeding program as it proceeds. For the polycross, recurrent selection, and reciprocal recurrent selection methods the different cycles of selection should be studied for numbers and proportions of genetically-superior individuals in the desirable class ranges of the frequency distribution and for genetic gains possible. The original breeding stocks and those varieties and strains that the breeding program is designed to replace should be included in these studies for purposes of comparison. Such studies would furnish information as to the progress being made and the advisability of continuing cycles of crossing followed by progeny testing and selection. Not often emphasized but probably of equal or more importance is the value of such studies to the plant breeder in the way of furnishing him inspiration and information necessary to keep abreast of his chosen field of endeavor.

One of the main purposes of this study was to determine at what level of soil fertility the breeding program should be conducted. The interactions between populations and fertilizer treatments so clearly evident in this article for both percentage sucrose and weight per root make it clear that the ideal would

be to conduct the breeding program at that level of soil fertility at which the commercial crop is to be grown. Obviously, due to the wide variety of soil fertility levels over which a commercial crop is grown and the wide variety of climatic and other conditions under which the commercial crop is produced, such a procedure is not practicable. However, it is quite clear from the results of this study that if the crop is to be grown at high fertility levels the breeding program should be conducted at the higher fertility levels.

Summary

1. Without exception a decrease in the parts per million of NO_3-N in the petioles was accompanied by an increase in percentage sucrose in the beet roots. These data were for replication group means. The same tendency in the replication group means was noted for the characters percentage sucrose and weight per root. As might be expected weight per root and parts per million of NO_3-N in the petioles were found to be positively associated. This same relation held for the comparisons involving treatment means. However the relation noted between percentage sucrose and parts per million of NO_3-N in the petioles for replication and treatment means was not so pronounced for population means.

2. Heterosis for percentage sucrose is definitely expressed in the F_1 hybrid between inbred lines 50-406 and 52-307. Tests conducted during the growing seasons of 1956 and 1957 indicate that heterosis for percentage sucrose is not uncommon in F_1 hybrids involving inbred lines of sugar beets.

3. It was found that percentage sucrose is not greatly reduced in the beet root when the parts per million of NO_3-N in the petioles is less than 1000 but is reduced when that amount is exceeded materially. These findings agree with those of Ulrich (16).

4. The first order interaction of populations $\times$ treatments for percentage sucrose was highly statistically significant and is of considerable biological interest. Populations A54-1, A54-1BB, and 50-406 grown on the fertilized plots have materially lower percentage sucrose than they do grown on the non-fertilized plots, whereas this is not true for populations 50-406BB, the F_1 hybrid, and 52-307. That is, on the average populations 50-406BB, the F_1 hybrid, and 52-307 produce as high a percentage sucrose on the fertilized plots as on the non-fertilized plots.

5. The first order interaction of populations × treatments for parts per million of NO_3-N in the petioles is illustrated by comparing populations A54-1BB and 50-406 for the two fertilizer treatments. The difference between treatments for A54-1BB is 3293 parts per million of NO_3-N in the petioles and for 50-406 is 1335. Also a comparison involving these same two populations and treatments illustrates the interaction for weight per root. The difference between treatments for A54-1BB is 0.93 pounds per root and for 50-406 is 0.27 pounds per root.

6. The interaction of replications × populations × treatments is significant at the one percent level for percentage sucrose and weight per root. The design of the experiment is not such as to provide an F value for testing the significance of this interaction for parts per million of NO_3-N in the petioles. However, for parts per million of NO_3-N in the petioles the first order interactions of replications × treatments and populations × treatments were statistically significant at the one percent levels and five percent levels, respectively.

The nature of the interaction of replications × populations × treatments for percentage sucrose is of interest. For the first three groups 50-406BB, the F_1 hybrid, and 52-307 show an increase in percentage sucrose on the fertilized plots, whereas the reverse is true for populations A54-1, A54-1BB, and 50-406.

On the non-fertilized plots A54-1 has an average of 588 parts per million of NO_3-N in the petioles for the first three replication groups and the average percent sucrose is 18.2. The same values for the F_1 hybrid for the first three replication groups on the fertilized plots are 630 and 18.3. Apparently A54-1 and the F_1 have the same optimum concentration of nitrogen in the petioles for maximum percentage sucrose in the roots. However, the F_1 hybrid reaches this optimum at the high fertility level, whereas A54-1 reaches approximately this same concentration of NO_3-N at the lower fertility level.

The behavior pattern of the F_1 and 52-307 is the same as regards the ability to produce the same percentage sucrose at the two levels of soil fertility. Hence this ability to produce the same percentage sucrose at the higher fertility level as at the lower fertility level is partially or completely dominant. On the other hand the 50-406 inbred is potentially the higher percentage sucrose parent as is shown by a comparison of 50-406 and 52-307 on the non-fertilized plots. The ability of 50-406 to produce a high percent of sucrose is at least partially if not completely dominant in the F_1 hybrid. The ability of the F_1 hybrid to react

as the inbred parent 50-406 in respect to high potential percentage sucrose production and as 52-307 parent in being able to react favorably to the higher fertility level in respect to percentage sucrose production results in the heterosis of the F_1 hybrid noted for the high fertility plots.

Another comparison of interest on the fertilized plots (see Table 8) involving the interaction of replications × populations × treatments is the relation between these three characters in replication groups 1 to 8 and 33 to 40. For all six populations there is a decrease in percentage sucrose and weight per root of replication group 33 to 40 compared with 1 to 8. There is a decided increase in parts per million of nitrate nitrogen in the petioles of group 33 to 40 as compared with group 1 to 8. Under conditions of this experiment the application of excesses of nitrogen results in a decided reduction of percentage sucrose and a slight reduction in weight per root.

7. For percentage sucrose and weight per root populations A54-1 and A54-1BB had considerably larger residual variances than any other populations. Population 50-406BB ranked next in this respect. Hence the greatest genetic variability would be expected in the populations of A54-1 and A54-1BB as regards both percentage sucrose and weight per root. On both fertilized and non-fertilized plots the residual variances for population A54-1BB were somewhat larger than the residual variances of A54-1. The reverse was true for weight per root but the differences are not as great.

8. The partitioning method was used to estimate the number and proportion of genetically-inferior and genetically-superior deviates in certain classes of the frequency distributions of populations A54-1 and A54-1BB. It was found that A54-1BB as compared with A54-1 possessed the greatest proportion of genetic deviates in the desirable classes on the fertilized plots whereas the reverse was true for these two populations grown on the non-fertilized plots. In the above comparisons percentage sucrose and weight per root were considered simultaneously.

9. Selections were made for high weight per root and high percentage sucrose from within 40 units of population A54-1 on non-fertilized plots. Each unit consisted of approximately 288 plants. The mean of A54-1 within the respective unit was used as the measurement to determine the odds against any selection made within a unit being a chance deviate. The 32 beets having the greatest odds taking into consideration both characters were grown in the greenhouse in a polycross plot.

A polycross progeny test revealed that the progenies of these 32 mother beets so selected surpassed A54-1 in yield of roots per acre and were the equal of A54-1 in percentage sucrose. The tests were conducted at a high fertility level, the land having received an application of 100 pounds of P_2O_5 and 200 pounds of N per acre. The progenies from two of the mother beets exceeded A54-1 in both weight of root and percentage sucrose. These results are important because they prove that the methods of selecting in small units and using an estimated environmental standard error, the mean of the unit, and the normal probability integral to establish odds are effective in isolating genetically-superior individuals. The progeny test as exemplified by the polycross method of breeding and which measures general combining ability confirmed the selection results and served to further identify genetically- superior individuals.

10. The importance to plant breeding programs of the methods employed and the findings reported are presented under "Discussion and Conclusions." It is evident that the methods employed also have considerable application in population genetic studies.

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Estimation by the Partitioning Method of the Numbers and Proportions of Genetic Deviates in Certain Classes of Frequency Distributions[1]

LEROY POWERS, D. W. ROBERTSON, AND A. G. CLARK[2]

In population genetic and plant breeding studies, methods, procedures, and formulas are needed for estimating the numbers and proportions of genetic deviates in classes of frequency distributions. Often population geneticists have need to estimate the number or proportion of individuals that occur in certain classes because of their genotype. The partitioning method of genetic analysis (Powers, et al, 9)[3] provides a means of so doing. In this article these individuals are designated as genetic deviates. Individuals occurring in the same classes because they are chance fluctuations from the mean of the population are designated as chance deviates. It is particularly important to the plant breeder to be able to determine the number and proportions of individuals in classes that are genetic deviates as contrasted to those that are chance deviates. The purposes of this article are to present and to illustrate the application of the partitioning method of genetic analysis to estimate the numbers and proportions of genetic deviates in certain classes of frequency distributions.

Design of Experiment

The design of the experiment is depicted by the tabulations of Table 1. There are two treatments which in this article are designated as "fertilized" and "non-fertilized." The fertilizer treatments are split plots of replications and are randomized within each replication. The six populations are randomized within each treatment. The locations refer to the position of the eight plants harvested from each plot. For more details of the experimental design see Powers, Robertson, Whitney, and Schmehl (11).

The populations are A54-1, A54-1BB, 50-406BB, 50-406, F_1 hybrid, and 52-307. A54-1, A54-1BB, and 50-406BB are heterogeneous and heterozygous. Populations 50-406 and 52-307 are inbreds and the F_1 is a hybrid between these two inbreds.

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[3] Numbers in parentheses refer to literature cited.

Table 1.—The Sources of Variation and the Number of Items for Each Source.[1]

Sources of Variation	Number of Items
Replications	40
Populations	6
Treatments	2
Locations	8

[1] The number of individuals per population within each treatment is 320.

Frequency Distributions

The frequency distributions of populations for percentage sucrose expressed in numbers are listed in Table 2 for the fertilized plots and Table 3 for the non-fertilized plots. The upper class limits of the tables are percentage sucrose. The frequency distributions of populations for weight per root expressed in numbers are listed in Table 4 for the fertilized plots and Table 5 for the non-fertilized plots. The number of plants per population is 320 within a treatment as stated in the footnote at the bottom of Table 1.

In a study of frequency distributions the investigator needs to determine which classes will provide the desired information. If the investigator is interested only in identifiable-genetically-superior individuals, then limits are set up such that the chances (odds) are in favor of only genetically-superior individuals occuring beyond those limits. Such being the requirements, usually a very few classes at one extreme of the frequency distribution are involved. The methods and procedures are those outlined by Powers (6, 8). Probably the most information is obtained by studying all the classes of the frequency distributions. This involves calculating the number of individuals in each class on the basis that they are chance deviates due to environmental variation. In other words, the calculated frequency distribution is based on the obtained mean of the population, the estimated environmental standard error, and tables of the normal probability integral. Methods, procedures, and formulas are given by Powers, et al (9) and Powers (4, 5, 6, and 8).

Formula

The formula giving the proportion of the individuals expected in a given class of the calculated frequency distribution

is $x = \frac{z - \bar{X}}{s_d}$. *See continuation of formula, page 681*

Table 2.—Means and Obtained and Calculated Frequency Distributions for Percentage Sucrose Expressed in Numbers, Fertilized Plots.[1]

Population and Distribution	Mean	Upper Limit of Class, Percent Sucrose														
		0 to 11.25	12.00	12.75	13.50	14.25	15.00	15.75	16.50	17.25	18.00	18.75	19.50	20.25	21.00	21.75 and over
	%	No.	No.	No.	No.	No.	No.	No.	No.	No.	No.	No.	No.	No.	No.	No.
A54-1																
Obtained	16.8	3	4	1	9	18	15	23	51	60	64	36	25	9	1	1
Calculated		0	0	1	4	10	23	41	57	60	54	37	20	9	3	1
A54-1BB																
Obtained	16.7	6	4	5	7	20	20	37	37	32	54	49	30	11	6	2
Calculated		0	0	2	4	12	26	42	58	62	51	34	18	8	2	1
50-406BB																
Obtained	17.3	2	1	5	6	10	17	19	30	42	73	55	35	15	8	2
Calculated		0	0	1	2	5	14	28	47	59	60	48	31	16	6	3
50-406																
Obtained	16.1	2	3	3	18	20	36	39	49	66	57	17	6	4		
Calculated		0	1	4	10	22	40	54	62	54	38	21	9	4	1	
F_1 hybrid																
Obtained	17.6		1	1	4	2	11	15	42	40	72	61	46	16	7	2
Calculated			0	0	1	4	10	22	40	54	62	54	38	21	9	5
52-307																
Obtained	16.6	2	3	1	9	12	27	27	53	67	67	33	14	2	3	
Calculated		0	0	2	5	13	28	45	59	60	50	32	16	7	2	1

[1] The estimated environmental standard error used in computing the calculated frequency distribution is 1.5392.

Table 3.—Means and Obtained and Calculated Frequency Distributions for Percentage Sucrose Expressed in Numbers, Non-Fertilized Plots.[1]

Population and Distribution	Mean	Upper Limit of Class, Percent Sucrose														
		0 to 11.25	12.00	12.75	13.50	14.25	15.00	15.75	16.50	17.25	18.00	18.75	19.50	20.25	21.00	21.75 and over
	%	No.	No.	No.	No.	No.	No.	No.	No.	No.	No.	No.	No.	No.	No.	No.
A54-1																
Obtained	17.9	3	1	0	1	4	12	11	25	36	62	66	58	26	11	4
Calculated		0	0	0	0	0	3	10	28	56	74	71	47	22	7	2
A54-1BB																
Obtained	17.8	1	3	2	4	8	9	13	24	42	61	38	62	30	17	6
Calculated		0	0	0	0	1	3	12	32	57	76	69	44	19	6	1
50-406BB																
Obtained	17.6		1	1	4	7	10	16	34	42	75	60	42	15	9	4
Calculated			0	0	0	1	4	16	38	64	78	63	36	15	4	1
50-406																
Obtained	17.4		1	1	4	4	7	19	42	50	82	58	38	11	3	
Calculated			0	0	0	2	7	20	46	70	76	56	29	11	3	
F_1 hybrid																
Obtained	17.6		0	1	1	1	6	11	27	72	85	66	38	9	1	2
Calculated			0	0	0	1	4	16	38	64	78	63	36	15	4	1
52-307																
Obtained	16.5	1	5	6	7	11	24	39	57	60	50	39	14	4	1	2
Calculated		0	0	0	2	9	25	51	73	73	51	25	9	2	0	0

[1] The estimated environmental standard error used in computing the calculated frequency distribution is 1.2279

Table 4.—Means and Obtained and Calculated Frequency Distributions for Weight Per Root Expressed in Numbers, Fertilized Plots.[1]

Population and Distribution	Mean	Upper Limit of Class, Pounds										
		0 to 0.5	1.0	1.5	2.0	2.5	3.0	3.5	4.0	4.5	5.0	5.5 and over
	lbs.	No.	No.	No.	No.	No.	No.	No.	No.	No.	No.	No.
A54-1												
Obtained	2.60	4	9	20	59	60	66	49	29	11	10	3
Calculated		1	3	16	44	78	86	59	25	7	1	0
A54-1BB												
Obtained	2.64	1	4	31	41	83	48	58	30	16	5	3
Calculated		0	3	14	42	76	85	62	28	8	2	0
50-406BB												
Obtained	2.04	2	17	47	88	94	51	15	4	1	1	
Calculated		2	13	46	91	94	54	17	3	0	0	
50-406												
Obtained	1.02	25	143	119	27	6						
Calculated		32	122	128	35	3						
F_1 hybrid												
Obtained	2.23	1	13	28	66	112	61	29	9	1		
Calculated		1	8	32	74	97	72	29	6	1		
52-307												
Obtained	1.16	18	103	124	70	5						
Calculated		22	93	134	62	9						

[1] The estimated environmental standard errors used in computing the calculated frequency distributions are listed in Table 9.

$\bar{x}$ = obtained mean of any population.
z = upper limit of any given class.
s_d = estimated standard error calculated from the estimated environmental variance (in this article for percentage sucrose the variance of the F_1).
x = x of Pearson's (3) tables, or X of Pearson's and Hartley's (2) tables.
$q = \frac{1}{2}(1 + a)$ of Pearsons (3) tables, or P (X) of Pearson's and Hartley's (2) tables.
$p = 1 - q$.

Means and Variances

From the above formula it can be seen that the means and variances of the different populations are required to compute the calculated frequency distributions listed in Tables 2, 3, 4, and 5. These calculated frequency distributions provide estimates of the number of individuals expected in the different classes due to fluctuations attributable to the environment. Then, the differences between the obtained and calculated frequency distribu-

Table 5.—Means, and Obtained and Calculated Frequency Distributions for Weight Per Root Expressed in Numbers, Non-Fertilized Plots.[1]

Population and Distribution	Mean	Upper Limit of Class, Pounds										
		0 to 0.5	1.0	1.5	2.0	2.5	3.0	3.5	4.0	4.5	5.0	5.5 and over
	lbs.	No.	No.	No.	No.	No.	No.	No.	No.	No.	No.	No.
A54-1												
Obtained	1.93	8	35	56	80	72	38	19	9	2		1
Calculated		3	17	57	99	90	42	10	2	0		0
A54-1BB												
Obtained	1.71	9	39	83	93	53	31	9	1	2		
Calculated		5	28	81	109	71	22	4	0	0		
50-406BB												
Obtained	1.40	11	60	123	79	37	9	1				
Calculated		11	57	117	99	32	4	0				
50-406												
Obtained	0.75	71	185	62	1	1						
Calculated		72	175	69	4	0						
F_1 hybrid												
Obtained	1.54	6	40	118	101	42	11	1	1			
Calculated		8	41	101	110	49	10	1	0			
52-307												
Obtained	0.58	155	129	35	1							
Calculated		116	194	10	0							

[1] The estimated environmental standard errors used in computing the calculated frequency distributions are listed in Table 9.

tions provide an estimate of the number of individuals in certain classes that are genetically-superior or, as the case may be, genetically-inferior to the mean of the population. These are termed genetic deviates.

The means and obtained variances are listed in Table 6. The variances are the total variances within populations, being based on 319 degrees of freedom.

One purpose of including the inbreds and F_1 hybrid in the study was to have estimates of the environmental variances. It is desirable to determine which provide the most reliable estimate of the environmental variances. A study of the means and variances listed in Table 6 furnish such information.

An analysis of variance of the variances for percentage sucrose revealed that there is a significant difference between population variances but not between replication variances, or between treatment variances (see Powers, Robertson, Whitney, and Schmehl, 11). None of the interactions involving the obtained variances are statistically significant.

Table 6.—Means and Obtained Variances for Percentage Sucrose, the Variances Being Based On 319 Degrees of Freedom.

Population	Fertilized		Non-Fertilized	
	Mean	Variance	Mean	Variance
A54-1	16.8	3.3072	17.9	2.8942
A54-1BB	16.7	4.9606	17.8	3.7654
50-406BB	17.3	3.4822	17.6	2.6291
50-406	16.1	2.7543	17.4	2.0138
F_1 hybrid[1]	17.6	2.3692	17.6	1.5077
52-307	16.6	2.5696	16.5	3.1126

[1] The standard errors calculated from the variances of the F_1 hybrid for the fertilized plots and the non-fertilized plots are 1.5392 and 1.2279, respectively.

On the fertilized plots there were significant differences between the variances of the non-segregating populations. That is, an analysis of variance for the variances of 50-406, F_1 hybrid, and 52-307 showed that the F value for populations had a P value less than 0.01. Also, the variances of the two inbreds as grown on the non-fertilized plots were significantly greater than the variance of the F_1 hybrid. This would not be expected if there were material genetic segregation within the two inbreds, as the variance of the F_1 should be high also. This is not believed to be due to any material genetic segregation within inbred lines but to the fact that they show more environmental variability, especially at the lower level of soil fertility. This increased environmental variability seems to be associated with lack of vigor of the inbreds. Data presented later support this conclusion.

Also, as can be seen from Table 6, there is for sucrose percentage no consistent relation between the variances and the means of either the segregating or non-segregating populations. The variances of the segregating populations, inbred 50-406, and the F_1 hybrid are larger on the fertilized plots than on the non-fertilized plots. The reverse is true of the variance of 52-307. From this consistency of behavior of the variances of the F_1 hybrid and because they are smaller than the variances of the two inbreds, it seems the variances of the F_1 hybrid provide the most reliable estimates of the environmental variances within a fertilizer treatment. It will be shown later that this conclusion is supported also by an analysis of the frequency distributions.

The standard errors calculated from the variances of the F_1 hybrid for the fertilized plots and the non-fertilized plots are 1.5392 and 1.2279, respectively. These are used as estimates of the environmental standard error in computing the calculated frequency distributions of Tables 2 and 3.

The means and variances for weight per root based on 319 degrees of freedom for the non-segregating populations arranged in ascending order of the magnitude of the means are listed in Table 7.

Table 7.—Treatments, Means, and Variances for Weight Per Root Based on 319 Degrees of Freedom for the Non-Segregating Populations Arranged in Ascending Order of the Magnitude of the Means.[1]

Population	Treatment	Mean x	Variance y
		Lbs.	
52-307	Non-fertilized	0.58	0.0976
50-406	Non-fertilized	0.75	0.0935
50-406	Fertilized	1.02	0.1593
52-307	Fertilized	1.16	0.1719
F_1 hybrid	Non-fertilized	1.54	0.2844
F_1 hybrid	Fertilized	2.23	0.4350

[1] Calculated from the above data, $m = 0.2171$, $b = -0.0565$, $\bar{x} = 1.2133$, and $\bar{y} = 0.2070$.

From an examination of Table 7 it can be determined that there is a positive relation between the means and variances, as was found by Powers, et al (10). Hence, the environmental variances may be estimated by regression of the variances on the means. The methods, procedures, and formula are those used by Powers (4, 6, 8) and Powers, et al (10). The values of m, b, $\bar{x}$, and $\bar{y}$ are given as a footnote of Table 7. The straight line regression of variances on the means of Table 7 accounts for 98.1 percent of the variability of the variances. Such being the case, apparently the relation is essentially linear. A t test reveals that the regression m (0.2171) is highly significant.

A comparison of the obtained variances with the estimated variances for the non-segregating generations (50-406, F_1 hybrid, and 52-307) provides evidence as to the reliability of the estimated environmental variances. The estimated environmental variances were computed by the methods and procedures given by Powers, Robertson, and Remmenga (10). In making the comparison possible bias is avoided by eliminating the mean and variance of the population whose environmental variances are being calculated from the estimate of the constants listed in the footnote of Table 7. For the segregating populations the regression employed in making the estimate was that computed from the six means and six variances listed in Table 7. For the non-segregating populations the regression employed in making the

estimate for a given population and treatment was that computed from the five means and five variances of the other populations and treatment.

The means, obtained variances, and estimated environmental variances for weight per root are listed in Table 8. The obtained variances are based on 319 degrees of freedom, being the total variances within a given population and treatment. A study of Table 8 reveals that as compared with the differences between the obtained variances and the corresponding estimated environmental variances of the segregating populations, the differences between the obtained variances and the corresponding estimated environmental variances of the non-segregating populations are small. It appears that the use of standard errors derived from the estimated environmental variances to compute the calculated frequency distributions of Tables 4 and 5 is justified. The standard errors calculated from estimated environmental variances are listed in Table 9.

Table 8.—Means, Obtained Variances, and Estimated Environmental Variances for Weight Per Root, the Obtained Variances Being Based on 319 Degrees of Freedom.

	Fertilized			Non-Fertilized		
		Variance			Variance	
Population	Mean	Obtained	Estimated[1]	Mean	Obtained	Estimated[1]
	Lbs.			Lbs.		
A54-1	2.60	0.9113	0.5080	1.93	0.6521	0.3626
A54-1BB	2.64	0.8064	0.5167	1.71	0.4937	0.3148
50-406BB	2.04	0.4345	0.3865	1.40	0.2802	0.2475
50-406	1.02	0.1593	0.1663	0.75	0.0935	0.1115
F_1 hybrid	2.23	0.4350	0.4067	1.54	0.2844	0.2760
52-307	1.16	0.1719	0.2001	0.58	0.0976	0.0514

[1] For the non-segregating populations the population involved has been excluded from the calculations of the regression used to compute the estimated variance.

Table 9.—Standard Errors for Weight Per Root Calculated from Estimated Environmental Variances of Table 8.

	Estimated	
Population	Fertilized	Non-Fertilized
A54-1	0.7128	0.6021
A54-1BB	0.7188	0.5611
50-406BB	0.6217	0.4975
50-406	0.4078	0.3339
F_1 hybrid	0.6378	0.5253
52-307	0.4473	0.2268

Analysis of Obtained and Calculated Frequency Distributions

The calculated frequency distributions of Tables 2, 3, 4, and 5 were computed from the corresponding means and environmental standard errors, the normal probability integral tables of Pearson (3), and the population n value per treatment of 320. The procedure is that outlined by Powers, et al (9). The standard errors used in computing the calculated frequency distributions for percentage sucrose are those of the F_1 hybrid given as a footnote at the bottom of Table 6. The standard errors used in computing the calculated frequency distributions for weight per root are those listed in Table 9. The details of computing the calculated frequency distributions are illustrated for percentage sucrose, using population A54-1.

For population A54-1 and class 1 of Table 2, $\bar{x} = 16.8$, $z = 11.25$, and $s_d = 1.5392$. As given previously the formula for computing x of Pearson's (3) tables of the normal probability integral is $x = \frac{z - \bar{x}}{s_d}$. By substitution $x = \frac{11.25 - 16.8}{1.5392} = \frac{-5.55}{1.5392}$ $= -3.61$. The value of q for an x value of -3.61 (see Pearson's, 3, Table 2) is 1.000 and p is $1 - 1.000 = 0.000$. The number of individuals expected in class 1 due to environmental variability is $0.000 \times 320 = 0.000$. Next consider the class having an upper class limit of 12.75. For this class $x = \frac{12.75 - 16.8}{1.5392} = \frac{-4.05}{1.5392} =$ -2.63. The value of $q = 0.996$ and $p = 1 - 0.996 = 0.004$. The number of individuals expected having values equal to or less than 12.75 percent sucrose is $0.004 \times 320 = 1.28$. Hence the number expected in the class having an upper limit of 12.75 is 1 as listed opposite population A54-1 in Table 2. The calculations for determining the number having values equal to or less than 16.50 are $x = \frac{16.50 - 16.80}{1.5392} = -0.19$. The value of $p = 0.425$ and the number of individuals expected to have values equal to or less than 16.50 is 136.00 (0.425×320). The calculations for the class having an upper limit of 17.25 is $x = \frac{17.25 - 16.80}{1.5392}$ $= 0.29$. The value of $q = 0.614$ and the number of individuals expected to have a value of 17.25 percent sucrose or less is $0.614 \times 320 = 196.48$. The number expected to fall in the class having an upper limit of 17.25 is $196.48 - 136.00 = 60.48$ (see above computations for an upper class limit of 16.50) which

rounded to whole numbers gives a value of 60 as listed in Table 2 for population A54-1. The number of individuals in the other classes of the calculated frequency distributions of Tables 2, 3, 4, and 5 was computed in a similar manner to the examples listed above for populations A54-1 and the character percentage sucrose. These examples encompass all the different computational situations that are likely to be encountered.

The obtained and calculated frequency distributions listed in Tables 2, 3, 4, and 5 provide the data necessary to estimate by the partitioning method of genetic analysis the number and proportions of individuals in classes of the obtained frequency distributions expected to be genetic deviates as compared with proportions that are expected to be chance deviates.

If the residual variances for any given population are significantly different from zero there should be more individuals in the extreme classes of the obtained frequency distribution of this population than in the corresponding classes of the calculated frequency distribution. Consider population A54-1 of Table 4. For the obtained frequency distribution the first four classes have more individuals, the next three classes fewer individuals and the last four classes more individuals than the corresponding groups of classes of the calculated frequency distribution. Hence the frequency distribution of A54-1 is divided into three groups by such a comparison of the obtained and calculated frequency distributions. In future discussion these three groups of classes will be designated as groups 1, 2, and 3, respectively.

A means of testing the reliability of any conclusions that may be drawn for the comparisons involving the corresponding obtained and calculated frequency distributions of Tables 2, 3, 4, and 5 is needed. To obtain a test of reliability the number of individuals within the classes of each of the three groups for each population was summed. The grouping for each population is shown by the perpendicular lines within the frequency distributions. Chi squares are computed to determine whether the differences noted between corresponding frequency distributions are greater than can be explained by chance. The chi square values and their corresponding p values are listed in Table 10.

The method of calculating homogeneity chi square will be illustrated for weight per root using the data for A54-1 grown on the fertilized plots. The obtained, calculated, and theoretical frequency distributions (based on three groups) for computing homogeneity chi square are listed in Table 11. Group 3 has the greatest weight per root. The standard formula for computing

Table 10.—Chi Square Test for Homogeneity and for Goodness of Fit of the Corresponding Obtained and Calculated Frequency Distributions of Tables 2, 3, 4, and 5 Grouped Into 3 Classes.[1]

Treatment	Percentage Sucrose		Weight of Root	
	Chi Square	P Lies Between	Chi Square	P Lies Between
Fertilized				
A54-1	11.657	0.01 and 0.00	15.466	0.01 and 0.00
A54-1BB	27.271	0.01 and 0.00	12.069	0.01 and 0.00
50-406BB	15.584	0.01 and 0.00	0.297	0.90 and 0.80
50-406	4.817	0.10 and 0.05	1.494	0.50 and 0.30
F_1 hybrid	5.369*	0.10 and 0.05	1.324	0.70 and 0.50
52-307	2.461	0.30 and 0.20	0.510	0.80 and 0.70
Non-fertilized				
A54-1	14.342	0.01 and 0.00	20.096	0.01 and 0.00
A54-1BB	33.164	0.01 and 0.00	8.914	0.02 and 0.01
50-406BB	9.211	0.01 and 0.00	1.991	0.50 and 0.30
50-406	2.140	0.50 and 0.30	0.876	0.70 and 0.50
F_1 hybrid	0.892*	0.70 and 0.50	0.262	0.90 and 0.80
52-307	18.481	0.01 and 0.00	33.388	0.01 and 0.00

[1] The degrees of freedom for chi square are 2.
*These are goodness of fit chi squares, all others are homogeneity chi squares.

homogeneity chi square is chi square $= 2\left\{ S\left(\frac{(T-0)^2}{T}\right)\right\}$.

By substitution in the formula chi square =

$$2\left(\frac{(14)^2}{78} + \frac{(24)^2}{199} + \frac{(10)^2}{43}\right)$$

$= 2(2.5128 + 2.8944 + 2.3256) = 15.4656$ which rounded to three places to the right of the decimal gives the value under weight per root and opposite sub-row-heading A54-1 under row heading fertilized. The other homogeneity chi square values were calculated by identical procedure.

Table 11.—Obtained, Calculated and Theoretical Frequency Distributions for Weight Per Root of A54-1 Grown on the Fertilized Plots, Classes Combined Into Three Groups.

Frequency Distribution	Group		
	1	2	3
Obtained	92	175	53
Calculated	64	223	33
Theoretical	78	199	43
T - 0 or C	14	—24	10

The method of calculating goodness of fit chi square will be illustrated for percentage sucrose using the data for F_1 hybrid grown on the nonfertilized plots. The obtained and calculated frequency distributions (based on three groups) for computing goodness of fit chi square are listed in Table 12. The standard formula for computing goodness of fit chi square is $S\left(\frac{(O-C)^2}{C}\right)$ By substituting the appropriate values in the formula we have $S\left(\frac{(1)^2}{21} + \frac{(7)^2}{243} + \frac{(6)^2}{56}\right) = 0.892$ as shown in Table 10.

Table 12.—Obtained and Calculated Frequency Distributions for Percentage Sucrose of F_1 Hybrid Grown on the Non-Fertilized Plots, Classes Combined Into Three Groups..

Frequency Distribution	Group 1	Group 2	Group 3
Obtained	20	250	50
Calculated	21	243	56
O - C	—1	7	—6

Table 10 furnishes additional evidence as to the nature of the residual variances of the segregating populations as compared with the residual variances of the non-segregating populations. A study of the chi square values for percentage sucrose listed in Table 10 reveals that the deviations between the obtained and calculated frequency distributions are greater than expected by chance for populations A54-1, A54-1BB and 50-406BB on the fertilized and non-fertilized plots. The same is true of weight of root for populations A54-1 and A54-1BB, but not for 50-406BB. None of the percentage-sucrose chi square values for 50-406, F_1 hybrid, and 52-307 grown on the fertilized plots indicate that the calculated frequency distributions deviate from their corresponding obtained frequency distributions more than would be expected by chance. The same is true for populations 50-406 and the F_1 hybrid on the non-fertilized plots. However, on the non-fertilized plots the chi square values for 52-307 for both percentage sucrose and weight per root are highly significant. On the fertilized plots in the higher classes of the frequency distribution there is no consistent increase of the obtained over the calculated as would be expected in the case of genetic variability; however there is a consistent increase of the obtained over the calculated for classes at the lower end of the curve. The

means of weight per root of 52-307 and 50-406 on the non-fertilized plots of 0.58 and 0.75 pounds as compared with 1.54 for the F_1 hybrid show the lack of vigor of these inbreds at the lower fertility level. It is believed that this accounts for the significant chi square value of 52-307 for percentage sucrose on the non-fertilized plots and the consistent increase of the obtained over the calculated for the higher classes of the frequency distribution. If such were due to genetic variability it would be expected to result in significant chi square values of 52-307 on the fertilized plots. Such was not the case. Furthermore, in no case are the chi square values of the F_1 significant, and the variance of the F_1 as previously pointed out was less than that of 52-307. Hence the use of the obtained variances of the F_1 hybrid as an estimate of the environmental variances for percentage sucrose seems justified.

The high chi square values of Table 10 with their accompanying P values indicate that probably the numerical differences in the higher classes of the frequency distributions between the obtained and calculated for populations A54-1 and A54-1BB are due primarily to genetic deviates. A study of the obtained and residual variances (Powers, et al, 10, Table 11) support this conclusion. The results of completing the partitioning of percentage sucrose for the higher classes (group 3) are given in Table 13. The values in this table resulted from subtracting the calculated values in Tables 2 and 3 from their corresponding obtained values.

Both the estimated number and percent of genetically-superior individuals in higher classes of the frequency distribution for percentage sucrose are listed in Table 13. To evaluate the data in this table a measure of the reliability of the following is needed: Numbers listed in the last column, differences noted between populations within treatments, and, finally, differences noted between treatments within populations. Test of reliability will be made by using the standard error of the binomial distribution. The formula used in estimating the standard error is $s_d = \sqrt{npq}$. The symbols have the following connotations.

n = the number of individuals in the population.

p = the proportion the individuals in the class under consideration are of the total.

$q = 1 - p$.

To test the reliability of the data listed in Table 13 the frequency distributions listed in Tables 2 and 3 are employed.

Table 13.—The Estimated Number and Percent of Genetically-Superior Individuals in Higher Classes of the Frequency Distribution, Percentage Sucrose.[1]

Treatment and Population	Upper Limit of Class, Percent						
	18.00	18.75	19.50	20.25	21.00	21.75 and Over	Total
Fertilized							
A54-1							
Number	10	—1	5	0	—2	0	12
Percent	15.6		20.0	0		0	8.8
A54-1BB							
Number	3	15	12	3	4	1	38
Percent	5.6	30.6	40.0	27.3	66.7	50.0	25.0
Non-fertilized							
A54-1							
Number			11	4	4	2	21
Percent			19.0	15.4	36.4	50.0	21.2
A54-1BB							
Number			18	11	11	5	45
Percent			29.0	36.7	64.7	83.3	39.1

[1] The percent of genetically-superior individuals is computed by dividing the number by the total of the class in which it occurs and multiplying by 100.

The procedure will be illustrated for A54-1 grown on the fertilized plots. The totals for the obtained and calculated in the higher classes of the frequency distribution (group 3) are 136 and 124, respectively, with an average of 130. The value of n is 320 and p is $130 \div 320 = 0.4062$. The value of $q = 1 - 0.4062 = 0.5938$. Substituting in the formula we have $s_d = \sqrt{(320)\ (0.4062)\ (0.5938)} = \sqrt{77.1845} = 8.79$. Hence the estimated standard error of 12, the total for A54-1 on the fertilized plots, is 8.79. Hence $12 \div 8.79 = 1.4$. A value of 1.4 has a P value of 0.16 according to Fisher's (1) table of x. Hence, this number (12) could well be a chance deviate from zero. The odds against the totals 38 (A54-1BB, fertilized), 21 (A54-1, non-fertilized), and 45 (A54-1BB, non-fertilized) being chance deviations from 0 are greater than 999:1 for each.

The next information to be derived from Table 13 pertains to the reliability of the differences between populations within treatments. Is the difference between 12 and 38, the number of estimated genetically-superior individuals for A54-1 and A54-1BB on the fertilized plots statistically significant? The average of these two values is $(12 + 38) \div 2 = 25$. The proportion is $25 \div 320 = 0.0781 = p$ and $q = 1 - 0.0781 = 0.9219$. Then $npq = (0.0781)\ (0.9219)\ (320) = 23.0401$ and $\sqrt{npq} = 4.80$. The difference between 12 and 25 or 38 and 25 is 13. The value

Table 14.—Goodness of Fit Chi Square for the Obtained and Calculated Frequency Distributions of the F_1 Hybrid, Fertilized Plots and Non-Fertilized Plots, Percentage Sucrose.[1]

Treatment and Distribution	Mean	Upper Limit of Class, Percent Sucrose														
		0 to 11.25	12.00	12.75	13.50	14.25	15.00	15.75	16.50	17.25	18.00	18.75	19.50	20.25	21.00	21.75 and Over
	%	No.	No.	No.	No.	No.	No.	No.	No.	No.	No.	No.	No.	No.	No.	No.
Fertilized																
Obtained	17.6		1	1	4	2	11	15	42	40	72	61	46	16	7	2
Calculated			0	0	1	4	10	22	40	54	62	54	38	21	9	5
Difference					4			—7	2	—14	10	7	8	—5		—5
Non-fertilized																
Obtained	17.6			1	1	1	6	11	27	72	85	66	38	9	1	2
Calculated				0	0	1	4	16	38	64	78	63	36	15	4	1
Difference						—1			—11	8	7	3	2		—8	

[1] The goodness of fit chi square for the fertilized plots is 14.2043, and P lies between 0.10 and 0.05. The goodness of fit chi square for the non-fertilized plots is 8.3140, and P lies between 0.30 and 0.20.

13 divided by its standard error (4.80) is 2.71. The odds against the values of 12 for A54-1 and 38 for A54-1BB being chance deviates from the mean of 25 is greater than 99:1. Similarly the difference between populations of the non-fertilized plots is significant.

The test to determine whether there are significant differences between treatments within populations is identical to that for determining whether the differences between populations within treatments is significant. For population A54-1 the values for the fertilized plots are 12 and 21. The mean is 16.5 and the standard error for the difference of 4.5 is 3.96. It is obvious that the two values of 12 and 21 cannot be considered as significantly different. However, this does not present the entire picture, as the estimate for A54-1 on the non-fertilized in the highest 3 classes is 10 whereas on the fertilized plots the corresponding estimate is 0. This difference can be shown to be highly significant.

The analyses for weight per root are performed in an identical manner and therefore need not be illustrated here. The presentation of the data and biological analyses are given by Powers, et al (11).

Partitioning the obtained frequency distributions to determine the numbers and proportions of genetically-inferior individuals in certain classes and the numbers and proportions of genetically-superior individuals in other classes is based on the assumption that the environmental variability is following the normal probability integral. It is desirable to ascertain if such is the case. For both percentage sucrose and weight per root it was shown that the variability of the F_1 was largely environmental. Hence tests conducted with the frequency distributions of this population would provide evidence as to whether the environmental variability for these characters does follow the normal probability integral. If for the F_1 population the corresponding obtained and calculated frequency distributions for percentage sucrose and weight per root do not differ more than would be expected by chance it can be assumed the environmental variability in these studies is following the normal probability integral. Such a conclusion is logical because the calculated frequency distributions were computed from the means, environmental standard errors, and tables of the normal probability integral. The test involves computing goodness of fit and homogeneity chi square.

The data for calculating the chi square values for percentage sucrose are given in Table 14 and for weight per root in Table 15. Goodness of fit chi squares are appropriate for making the test of the data for percentage sucrose. The reason for this is that

Table 15.—Homogeneity Chi Square for the Obtained and Calculated Frequency Distributions of the F_1 Hybrid, Fertilized Plots and Non-Fertilized Plots, Weight Per Root.[1]

Treatment and Distrbuton	Mean	Upper Limit of Class, Pounds								
		0 to 0.5	1.0	1.5	2.0	2.5	3.0	3.5	4.0	4.5
	lbs.	No.	No.	No.	No.	No.	No.	No.	No.	No.
Fertilized										
Obtained	2.23	1	13	28	66	112	61	29	9	1
Calculated		1	8	32	74	97	72	29	6	1
Theoretical			11.5	30	70	104.5	66.5	37.5		
Difference			—2.5	2	4	—7.5	5.5	—1.5		
Non-fertilized										
Obtained	1.54	6	40	118	101	42	11	1	1	
Calculated		8	41	101	110	49	10	1	0	
Theoretical			47.5	109.5	105.5	45.5	12			
Difference			1.5	—8.5	4.5	3.5	—1			

[1] The homogeneity chi square values for the fertilized plots is 3.9172 and for the non-fertilized plots is 2.5032. The P values lie between 0.70 and 0.50 for both chi squares.

the environmental standard error employed in computing the calculated frequency distributions was derived from the F_1 data. For the weight per root frequency distributions given in Table 15, the F_1 data for the fertilizer treatment under consideration did not enter into the estimation of the environmental standard error used in computing the calculated frequency distributions. Therefore homogeneity chi squares are appropriate for testing whether the environmental variability is following the normal probability integral.

Goodness of fit chi square for the fertilized plot of Table 14 $= (4)^2/15 + (7)^2/22 + (2)^2/40 + (14)^2/54 + (10)^2/62 + (7)^2/54 + (8)^2/38 + (5)^2/21 + (5)^2/14 = 14.2043$. Homogeneity chi square for the fertilized plot of table 15 $= 2[(2.5)^2/11.5 + (2)^2/30 + (4)^2/70 + (7.5)^2/104.5 + (5.5)^2/66.5 + (1.5)^2/37.5] = 3.9172$. None of the chi square values have P values as low as 0.05. It may be concluded that the environmental variability of the F_1 hybrid is following the normal probability integral. Furthermore the use of regression in estimating the environmental variance of the F_1 hybrid is reliable. Otherwise the obtained and calculated frequency dstributions should have differed more than expected due to chance fluctuations.

Discussion and Summary

1. The application of methods, procedures, and formulas for estimating the proportion of genetically-inferior and genetically-superior individuals in certain classes of the obtained frequency

distributions of segregating populations is illustrated. The details of the computations are given.

2. The computation of the calculated frequency distributions is based on obtained means of the populations, the estimated environmental standard errors, and tables of the normal probability integral. Methods of determining the reliability of the estimated environmental standard errors are illustrated. Whether the environmental variability is following the normal probability integral can be determined by comparing the obtained and calculated frequency distributions of the non-segregating populations whose residual variances are not significantly different from zero. For those non-segregating populations whose residual variances are significantly different from zero the test for normality would need to be made by employing standard errors computed from their respective obtained variances. If the deviations between the obtained and calculated frequency distributions are no greater than expected by chance, the environmental variability is following the normal probability integral. Chi square may be used to test whether the deviations between the frequency distributions are greater than would be expected by chance (see Powers, 5). The procedure is illustrated for the F_1 hybrid, which provided reliable estimates of the environmental variance for both percentage sucrose and weight per root.

3. For weight per root, regression of the variances on the means of the non-segregating populations is employed in estimating the environmental variances of the segregating populations. The detailed procedures used and the justification for these procedures are given by Powers, Robertson, and Remmenga (10).

4. The techniques outlined in this article involve partitioning the obtained frequency distributions into three rather well defined groups: Genetically-inferior, mediocre, and genetically-superior individuals. There is overlapping of these groups and the partitioning is not complete. That is, the numbers and proportions are underestimates of the genetically-inferior and genetically-superior individuals for those classes having values closer to the mean of the population. The proportions estimated for the extreme classes of the frequency distribution are fairly accurate estimates for the genetically-superior individuals as regards percentage sucrose and weight per root.

5. The variance of the F_1 hybrid furnishes a rather reliable estimate of the environmental variability for percentage sucrose. In those cases including some genetic variability in the estimation of the environmental variance, the standard errors used in computing the calculated frequency distribution would be some-

what larger than the true environmental standard errors. Hence, the estimates of the number of genetic deviates in the classes at the extremes of the frequency distributions would be underestimates. That is, the numbers and proportions of the genetically-superior individuals in the desirable classes would be somewhat greater than the estimates indicate. Hence in their application to plant breeding, in the event that some genetic variability is included in estimating the environmental variances, the methods and procedures provide conservative estimates.

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Estimation of the Environmental Variances and Testing Reliability of Residual Variances for Weight per Root in Sugar Beets[1]

LeRoy Powers, D. W. Robertson, and E. E. Remmenga[2]

In genetic studies of quantitative characters such as weight per root in sugar beets (*Beta vulgaris* L.) often there is a positive relation between the means and variances. Powers (1)[3] described a method of estimating the environmental variances in quantitative studies on tomatoes. The method illustrated here is essentially that described previously but is applied to population genetic studies at different levels of soil fertility. There has been considerable inquiry as to the details of the methods and procedures involved in calculating the environmental variances and in testing the reliability of the residual variances. The purposes of this article are: 1. to illustrate in detail the methods, procedures, and formulas used in estimating the environmental variances and 2. to illustrate methods used in testing the reliability of the residual variances obtained by subtracting the estimated environmental variances from the obtained variances.

Design of Experiment

The design of the experiment may be readily depicted by the tabulations listed in Table 1. There are two treatments which in this article will be designated as "fertilized" and "nonfertilized." The fertilizer treatments are split plots of replications and are randomized within each replication. The six populations are randomized within each treatment. The locations refer to the position of the eight plants harvested from each plot. For more details of the experimental design see Powers, Robertson, Whitney, and Schmehl (2).

Table 1.—The Sources of Variation and the Number of Items for Each Source.

Source of Variation	Number of Items
Replications	40
Populations	6
Treatments	2
Locations	8

[1] Cooperative investigations of the Crops Research Division, Agricultural Research Service, U. S. Department of Agriculture, the Colorado Agricultural Experiment Station, and the Beet Sugar Development Foundation. Approved by the Colorado Agricultural Experiment Station for publication as Scientific Series Article No. 553.

[2] Geneticist, Crops Research Division, Agricultural Research Service, U. S. Department of Agriculture, Professor and Head, Department of Agronomy, Colorado State University, and Assistant Professor of Mathematics, Colorado State University, respectively.

[3] Numbers in parentheses refer to literature cited.

The populations are A54-1, A54-1BB, 50-406BB, 50-406, F_1 hybrid, and 52-307. A54-1, A54-1BB, and 50-406BB are heterogeneous and heterozygous. Populations 50-406 and 52-307 are inbreds and the F_1 is a hybrid between these two inbreds.

Estimation of the Environmental Variances

To illustrate the methods, procedures and application of the formulas used in estimating the environmental variances and in testing the reliability of the residual variances the within plot environmental variances [(R X L) + L] with 280 degrees of freedom will be used.

One of the first steps is to determine the relation between the means and variances within populations and treatments. An analysis of variance must have been made which includes a within replication, population, and treatment breakdown. The means and within plot variances [(R X L) + L] for populations and treatments of the non-segregating generations are listed in Table 2.

Table 2.—Means, Within Plot Variances [(R X L) + L], Regressions, and Points of Intercept of Weight Per Root Arranged in Ascending Order of the Magnitude of the Means for the Non-Segregating Populations and Treatments..

Population	Treatment	Mean (X)	Variance [(R X L) + L] (Y)	Regression of Y on X (m)	Point of Intercept (b)
		Lbs.			
52-307	Non-fertilized	0.58	0.0535	0.170146	—0.042516
50-406	Non-fertilized	0.75	0.0776	0.168697	—0.039658
50-406	Fertilized	1.02	0.1398	0.172331	—0.047538
52-307	Fertilized	1.16	0.1586	0.171239	—0.045137
F_1 hybrid	Non-fertilized	1.54	0.2144	0.172255	—0.044449
F_1 hybrid	Fertilized	2.23	0.3370	0.172013	—0.044953

A study of Table 2 reveals that the means and the within plot variances are positively associated and that probably the relation is essentially a straight line. This suggests using linear regression of the within plot variances [(R X L) + L] on the means of the non-segregating populations and treatments to estimate the environmental variances. The details of the calculations are shown in Table 3.

The following information can be obtained from Table 3. The t test shows that the regression value 0.171087 is significantly different from zero at the one percent level. The degrees of freedom for testing t are n-2 = 4. Also from the figures given opposite the row heading $S_{dy \cdot x}{}^2$ it can be calculated that the regression of mean weight per root accounts for 99.7 percent [(0.052580 ÷ 0.052757) X 100] of the sums of squares for variances. Since

Table 3.—Computation of Regression of the Within-Plot Variances [(R X L) + L] on the Means, the Means and Variances Being Listed in Table 2.

$SX = 7.28$	$SY = 0.9809$	$n = 6$
$\bar{x} = 1.213333$	$\bar{y} = 0.163483$	
$SX^2 = 10.6294$	$SY^2 = 0.213118$	$SXY = 1.497488$
$(SX)^2/n = 8.833067$	$(SY)^2/n = 0.160361$	$(SX)(SY)/n = 1.190159$
$Sx^2 = 1.796333$	$Sy^2 = 0.052757$	$Sxy = 0.307329$

$\text{Regression} = Sxy/Sx^2 = 0.307329 \div 1.796333 = 0.171087 = m$

$S_{dy.x^2} = Sy^2 - (Sxy)^2/Sx^2 = 0.052757 - (0.307329)^2/1.796333$
$= 0.052757 - 0.052580 = 0.000177$

$s_{y.x^2} = S_{dy.x^2}/(n-2) = 0.000177/4 = 0.000044$

$s_m^2 = s_{y.x^2}/Sx^2 = 0.000024$

$s_m = \sqrt{0.000024} = 0.0049$

$t = m\text{-}0/s_m = 0.171087/0.0049 = 34.9157$

P is less than 0.01

such a high percentage (99.7%) of the sums of squares calculated from the variances of Table 3 is accounted for by regression it follows that the relation between the means and variances must be essentially linear. A study of the frequency distribution of the plot means and variances of population A54-1 showed that this linear relation held for the populations having higher mean values for weight per root.

In estimating the environmental variances the formula $y = mx + b$ is employed. This is the same formula used by Powers (1) and gives the same results as the formula employed by Snedecor (3, p. 112). The symbols have the following connotation.

- y = the estimated environmental variance.
- m = the slope of the regression line (regression of the within plot variances on the means).
- x = the mean weight per root of the population whose variance is being estimated.
- b = the point at which the regression line intercepts the ordinate.

From Table 3 it can be seen that $y = 0.163483$, $m = 0.171087$, and $x = 1.213333$. The value of b is calculated from the formula $b = y - mx$ using the values of y, m, and x given in the immediately preceding sentence. By substituting the appropriate values in the formula $b = y - mx$, we have: $b = 0.163483 - [(0.171087)\ (1.213333)] = -0.044103$.

In Table 4 are listed the means and within plot obtained, estimated, and residual variances for populations and treatments.

Table 4.—Means and Within Plot Obtained, Estimated, and Residual Variances of Weight Per Root in Pounds for Populations and Treatments.

Population	Mean	Variance		
		Obtained	Estimated	Residual
	Lbs.			
Fertilized				
A54-1	2.60	0.8691	0.4007	0.4684
A54-1BB	2.64	0.7640	0.4076	0.3564
50-406BB	2.04	0.4033	0.3049	0.0984
50-406	1.02	0.1398	0.1282	0.0116
F_1 hybrid	2.23	0.3370	0.3386	—0.0016
52-307	1.16	0.1586	0.1535	0.0051
Non-fertilized				
A54-1	1.93	0.5412	0.2861	0.2551
A54-1BB	1.71	0.3950	0.2485	0.1465
50-406BB	1.40	0.2279	0.1954	0.0325
50-406	0.75	0.0776	0.0869	—0.0093
F_1 hybrid	1.54	0.2144	0.2208	—0.0064
52-307	0.58	0.0535	0.0562	—0.0027

The procedures for calculating the estimated environmental variances of Table 4 will be illustrated for population A54-1 fertilized. Substituting in the formula $y = mx + b$ we have: $y = (0.171087)\,2.60 + (-0.044103) = 0.400723$ as shown in the fourth column of Table 4. The estimated environmental variances for the other populations in Table 4 were calculated in an identical manner. However, for populations 50-406, F_1 hybrid, and 52-307 the mean and variance of the population whose environmental variance is being estimated were not used in calculating m and b (see Table 2). Hence the value of n is 5 and degrees of freedom are 3 in these cases.

Testing the Reliability of the Residual Variances

The residual variances of Table 4 were obtained by subtracting the estimated environmental variances from their corresponding obtained variances. A measure of the reliability of the residual variances is needed. Such a test of reliability of residual variances is obtained by estimating the environmental variance for each replication and then computing the standard analysis of variance involving the obtained and estimated environmental variances. Replication and treatment effects are removed by this analysis. The procedure is illustrated for population 50-406BB.

In Table 5 (see appendix) are listed the means, obtained variances, and estimated environmental variances for replications and treatments, population 50-406BB. The means are used in the estimation of the environmental variances for each replication and treatment. The procedure for estimating the environmental variances of Table 5 is that employed in calculating the environmental variances of Table 4. The formula $y = mx + b$ is employed; m is obtained from Table 3; x is obtained from Table 5, row heading 1, column 2; and as before b is –0.044103. By substitution in the formula for replication 1, fertilized, $y = (0.171087)(1.87) + (-0.044103) = 0.2758$ as listed in the fourth column opposite row heading 1 of Table 5. The other values for the estimated variances of Table 5 were calculated in an identical manner.

In Tables 5, 6, 7, and 8 of the appendix are listed the detailed data from which are calculated analyses of variance of the obtained and estimated variances for population 50-406BB. The data for replications, treatments, and variances are listed in Table 5. The totals of variances within replications and treatments are listed in Table 6, the totals of treatments within replications and variances in Table 7, and the totals of replications within treatments and variances in Table 8. The totals of columns and the sums of Xs squared for columns are listed at the bottoms of Tables 5 to 8, inclusive. Also the appropriate column totals squared and summed are given at the bottoms of these same four tables.

Table 9 of the appendix illustrates the detailed calculations and gives the analysis of variance of the obtained and estimated variances for population 50-406BB. The sums of the Xs squared for replications is taken from the bottom of Table 6 (see last column), for variances from the bottom of Table 7 (see SX_v^2), and for treatments from the bottom of Table 8 (see last column). The values SX^2 of Table 9 for R X V, R X T, and V X T were obtained by summing the first two SX^2 values listed at the bottoms of Tables 7, 6, and 8, respectively. The value SX^2 of Table 9 for R X V X T was obtained by totaling the four values listed opposite SX^2 at the bottom of Table 5.

The procedure for calculating the analysis of variance of Table 9 is standard and the data in Table 9 are given in sufficient detail so that anyone desiring to do so can follow the calculations.

The purpose of the analysis of variance of the obtained and estimated environmental variances listed in Table 9 was to determine whether the residual variances for 50-406BB listed in

Table 4 are significantly greater than zero. It can be determined by comparing the obtained F value for variances with the F value for the one percent level that the average estimated variance of the two fertilizer treatments in Table 4 for 50-406BB is significantly smaller than the corresponding average of the two obtained variances. Hence it follows that the average of these two residual variances would be significantly greater than zero. It is clear that these results could be due to only one of these residual variances being significantly greater than zero. To determine whether such might be the case the analyses of variance given in Tables 10 and 11 were calculated. These are within treatments and were calculated from the data given in Table 5. With the exception that the analysis is for each treatment the procedure is that outlined for the analysis given in Table 9. The F value for variances calculated for the fertilized plots, Table 10, is significant at the one percent level, whereas the corresponding F value for the non-fertilized plots is not significant at the five percent level. It follows that considerable confidence can be placed in the conclusion that the residual variance for 50-406BB as grown on the fertilized plots is significantly greater than zero, whereas, by itself, little confidence could be placed in the conclusion that the residual variance for 50-406BB as grown on the non-fertilized plots is significantly greater than zero.

The procedure for testing whether the residual variance of any given population within a given fertilizer treatment is different from zero, is identical to that given above for 50-406BB.

The data in Table 4 provide a means of determining the reliability of the methods employed in estimating the environmental variances. The residual variances of the non-segregating populations (50-406, F_1 hybrid, and 52-307) provide the means of so doing. The estimated environmental variances listed in the fourth column of Table 4 were calculated from the means, and m and b values listed in Table 2. It will be recalled that the m and b values were estimated from the five means and variances of that same table, omitting the mean and variance of the population whose environmental variance is being estimated. Taking a specific example, in the row heading "52-307 non-fertilized" of Table 2, the values of 0.170146 and –0.042516 were calculated from the other five means of the table, omitting the mean 0.58 and and the variance 0.0535. Hence, the estimated environmental variances of Table 4 are (due to the manner of estimating) independent of their respective obtained variances for any given population. Such being the case a means of testing the reliability of the methods employed in estimating the environmental variances is provided. For example, if the residual

variances are not significantly greater than zero considerable confidence can be placed in using the populations so employed to estimate the environmental variances of those populations whose obtained variances are being analyzed. In this article these populations (A54-1, A54-1BB, and 50-406BB) are designated as the segregating populations.

Conclusions and Summary

1. The environmental variances are estimated by the use of regression (see Powers, 1).

2. By assuming that regression is a straight line relation 99.7 percent of the variability between variances of Table 2 is accounted for by the regression of the variances on the means of that same table. It follows that the relation between the variances and means is essentially linear.

3. An analysis of variance of the obtained and estimated environmental variances for replications, populations and treatments is used to test whether the residual variances are significantly different from zero. However, as was the case in this article, it may be necessary to make the calculations within treatments for a given population or populations. This method of testing the significance of residual variances removes effects due to replications and treatments.

4. In some studies it might be desirable to include all the segregating populations in the calculations. The methods, procedures, and application of the formula apply equally well if such populations are included. Also in some studies it may be desirable to estimate the environmental variances of the non-segregating generations and employ an analysis of variance to determine if they are significantly different. Such a test can be made readily by employing the methods and procedures outlined in this article.

5. The methods, procedures, and formula employed are equally applicable to a wide variety of genetic studies involving quantitative characters.

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Appendix

The appendix includes those tables listing the data necessary to make the detailed calculations outlined in the text.

Table 5.—The Means, Obtained Variances, and Estimated Environmental Variances for Replications and Treatments, Population 50-406BB.

Replication	Fertilized			Non-Fertilized		
	Mean	Variance		Mean	Variance	
		Obtained	Estimated		Obtained	Estimated
1	1.87	0.3477	0.2758	1.62	0.1560	0.2331
2	2.09	0.4095	0.3135	1.46	0.3417	0.2057
3	2.27	0.2239	0.3443	1.51	0.1658	0.2142
4	1.88	0.3218	0.2775	1.45	0.7555	0.2040
5	2.28	0.5237	0.3460	1.49	0.2505	0.2108
6	2.13	0.1372	0.3203	1.41	0.1196	0.1971
7	1.90	0.2370	0.2810	1.24	0.0796	0.1681
8	2.28	0.4680	0.3460	1.35	0.0497	0.1869
9	2.02	0.3061	0.3015	2.16	0.1486	0.3255
10	2.64	0.9163	0.4076	1.41	0.4216	0.1971
11	2.33	0.1986	0.3545	1.30	0.0711	0.1783
12	2.32	0.0900	0.3528	1.36	0.1642	0.1886
13	1.94	0.4702	0.2878	1.31	0.0355	0.1800
14	2.57	0.9052	0.3956	1.22	0.3027	0.1646
15	1.90	0.2169	0.2810	1.49	0.1981	0.2108
16	2.20	0.0684	0.3323	1.16	0.1395	0.1544
17	2.14	0.2867	0.3220	1.17	0.2301	0.1561
18	1.45	0.2214	0.2040	1.34	0.1921	0.1852
19	2.33	0.5057	0.3545	1.39	0.4174	0.1937
20	2.35	0.6142	0.3580	0.86	0.2008	0.1030
21	1.78	0.2949	0.2604	1.09	0.4323	0.1424
22	2.14	0.3805	0.3220	0.99	0.1662	0.1253
23	2.05	0.4875	0.3066	1.42	0.0655	0.1988
24	2.35	0.6041	0.3580	1.33	0.1627	0.1834
25	2.07	0.2890	0.3101	1.06	0.2847	0.1373
26	1.92	0.4905	0.2844	1.47	0.1065	0.2074
27	1.67	0.4085	0.2416	1.42	0.5811	0.1988
28	2.10	0.3524	0.3152	1.03	0.1303	0.1321
29	1.40	0.4177	0.1954	1.09	0.2501	0.1424
30	1.78	0.2860	0.2604	1.73	0.2584	0.2519
31	1.87	0.2203	0.2758	1.07	0.0773	0.1390
32	1.75	0.5077	0.2553	1.95	0.3434	0.2895
33	1.93	0.5301	0.2861	1.88	0.1165	0.2775
34	1.83	0.4769	0.2690	1.15	0.0950	0.1527
35	2.53	1.0797	0.3888	1.23	0.0761	0.1663
36	1.68	0.2755	0.2433	1.37	0.2703	0.1903
37	1.84	0.4249	0.2707	1.53	0.4414	0.2177
38	2.30	0.4635	0.3494	1.70	0.1044	0.2468
39	1.80	0.4474	0.2639	1.95	0.3052	0.2895
40	1.80	0.2250	0.2639	1.81	0.4072	0.2656
SX		16.1306	12.1763		9.1147	7.8119
SX^2		8.256109	3.800786		3.024735	1.619029

$SX_{vt}^2 = 552.562076$

Table 6.—The Totals of Variances Within Replications and Treatments, Population 50-406BB.

Replication	Treatments		Totals of Treatments
	Fertilized	Non-Fertilized	
1	0.6235	0.3891	1.0126
2	0.7230	0.5474	1.2704
3	0.5682	0.3800	0.9482
4	0.5993	0.9595	1.5588
5	0.8697	0.4613	1.3310
6	0.4575	0.3167	0.7742
7	0.5180	0.2477	0.7657
8	0.8140	0.2366	1.0506
9	0.6076	0.4741	1.0817
10	1.3239	0.6187	1.9426
11	0.5531	0.2494	0.8025
12	0.4428	0.3528	0.7956
13	0.7580	0.2155	0.9735
14	1.3008	0.4673	1.7681
15	0.4979	0.4089	0.9068
16	0.4007	0.2939	0.6946
17	0.6087	0.3862	0.9949
18	0.4254	0.3773	0.8027
19	0.8602	0.6111	1.4713
20	0.9722	0.3038	1.2760
21	0.5553	0.5747	1.1300
22	0.7025	0.2915	0.9940
23	0.7941	0.2643	1.0584
24	0.9621	0.3461	1.3082
25	0.5991	0.4220	1.0211
26	0.7749	0.3139	1.0888
27	0.6501	0.7799	1.4300
28	0.6676	0.2624	0.9300
29	0.6131	0.3925	1.0056
30	0.5464	0.5103	1.0567
31	0.4961	0.2163	0.7124
32	0.7630	0.6329	1.3959
33	0.8162	0.3940	1.2102
34	0.7459	0.2477	0.9936
35	1.4685	0.2424	1.7109
36	0.5188	0.4606	0.9794
37	0.6956	0.6591	1.3547
38	0.8129	0.3512	1.1641
39	0.7113	0.5947	1.3060
40	0.4889	0.6728	1.1617
ΣX	28.3069	16.9266	45.2335
ΣX^2	22.252052	8.288376	54.457776

Table 7.—The Totals of Treatments Within Replications and Variances, Population 50-406BB.

Replication	Variance		Total of Variances
	Obtained	Estimated	
1	0.5037	0.5089	1.0126
2	0.7512	0.5192	1.2704
3	0.3897	0.5585	0.9482
4	1.0773	0.4815	1.5588
5	0.7742	0.5568	1.3310
6	0.2568	0.5174	0.7742
7	0.3166	0.4491	0.7657
8	0.5177	0.5329	1.0506
9	0.4547	0.6270	1.0817
10	1.3379	0.6047	1.9426
11	0.2697	0.5328	0.8025
12	0.2542	0.5414	0.7956
13	0.5057	0.4678	0.9735
14	1.2079	0.5602	1.7681
15	0.4150	0.4918	0.9068
16	0.2079	0.4867	0.6946
17	0.5168	0.4781	0.9949
18	0.4135	0.3892	0.8027
19	0.9231	0.5482	1.4713
20	0.8150	0.4610	1.2760
21	0.7272	0.4028	1.1300
22	0.5467	0.4473	0.9940
23	0.5530	0.5054	1.0584
24	0.7668	0.5414	1.3082
25	0.5737	0.4474	1.0211
26	0.5970	0.4918	1.0888
27	0.9896	0.4404	1.4300
28	0.4827	0.4473	0.9300
29	0.6678	0.3378	1.0056
30	0.5444	0.5123	1.0567
31	0.2976	0.4148	0.7124
32	0.8511	0.5448	1.3959
33	0.6466	0.5636	1.2102
34	0.5719	0.4217	0.9936
35	1.1558	0.5551	1.7109
36	0.5458	0.4336	0.9794
37	0.8663	0.4884	1.3547
38	0.5679	0.5962	1.1641
39	0.7526	0.5534	1.3060
40	0.6322	0.5295	1.1617
SX	25.2453	19.9882	45.2335
SX^2	18.775334	10.140590	54.457776

$SXv^2 = 1036.853311$

Table 8.—The Totals of Replications Within Variances and Treatments, Population 50-406BB.

Treatment	Variance		Total of Treatments
	Obtained	Estimated	
Fertilized	16.1306	12.1763	28.3069
Non-fertilized	9.1147	7.8119	16.9266
SX	25.2453	19.9882	45.2335
SX^2	343.274013	209.288063	1087.790375

Table 9.—Analysis of Variance of the Obtained and Estimated Environmental Variances for Population 50-406BB and Weight of Root[1].

Source of Variation	SX^2	Number of Items	$SX^2 \div$ Number of Items	Sx^2	Degrees of Freedom	Mean Square	F Value	F Value for P = 0.05	F Value for P = 0.01
Replications	54.457776	4	13.614444	0.826509	39	0.021193	1.52	1.71	2.14
Variances	1036.853311	80	12.960666	0.172731	1	0.172731	12.41	4.10	7.35
Treatments	1087.790375	80	13.597380	0.809445	1	0.809445	58.14	4.10	7.35
R X V	28.915924	2	14.457962	0.670787	39	0.017200	1.24	1.71	2.14
R X T	30.540428	2	15.270214	0.846325	39	0.021701	1.56	1.71	2.14
V X T	552.562076	40	13.814052	0.043941	1	0.043941	3.16	4.10	7.35
R X V X T	16.700659			0.542986	39	0.013923			
Total	16.700659	1	16.700659	3.912724	159				

[1] The correction factor $= (45.2335)^2 \div 160 = 12.787935$

Table 10.—Analysis of Variance for the Obtained and Estimated Environmental Variances for Population 50-406BB, Weight of Root, Fertilized[1].

Source of Variation	SX^2	Number of Items	$SX^2 \div$ Number of Items	Sx^2	Degrees of Freedom	Mean Square	F Value	F Value for P = 0.05	F Value for P = 0.01
Replications	22.252052	2	11.126026	1.110019	39	0.028462	1.51	1.71	2.14
Variances	408.458538	40	10.211463	0.195456	1	0.195456	10.37	4.10	7.35
R X V				0.735413	39	0.018857			
Total	12.056895	1	12.056895	2.040888	79				

[1] The correction factor = $(28.3069)^2 \div 80 = 10.016007$

Table 11.—Analysis of Variance for the Obtained and Estimated Environmental Variances for Population 50-406BB, Weight of Root, Non-Fertilized[1].

Source of Variation	SX^2	Number of Items	$SX^2 \div$ Number of Items	Sx^2	Degrees of Freedom	Mean Square	F Value	F Value for P = 0.05	F Value for P = 0.01
Replications	8.288376	2	4.144188	0.562816	39	0.014431	1.18	1.71	2.14
Variances	144.103538	40	3.602588	0.021216	1	0.021216	1.73	4.10	7.35
R X V				0.478360	39	0.012266			
Total	4.643764	1	4.643764	1.062392	79				

[1] The correction facor = $(16.9266)^2 \div 80 = 3.581372$

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